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Monograph of the North American Species of Deraeocoris—Heteroptera Miridae

By Harry H. Knight
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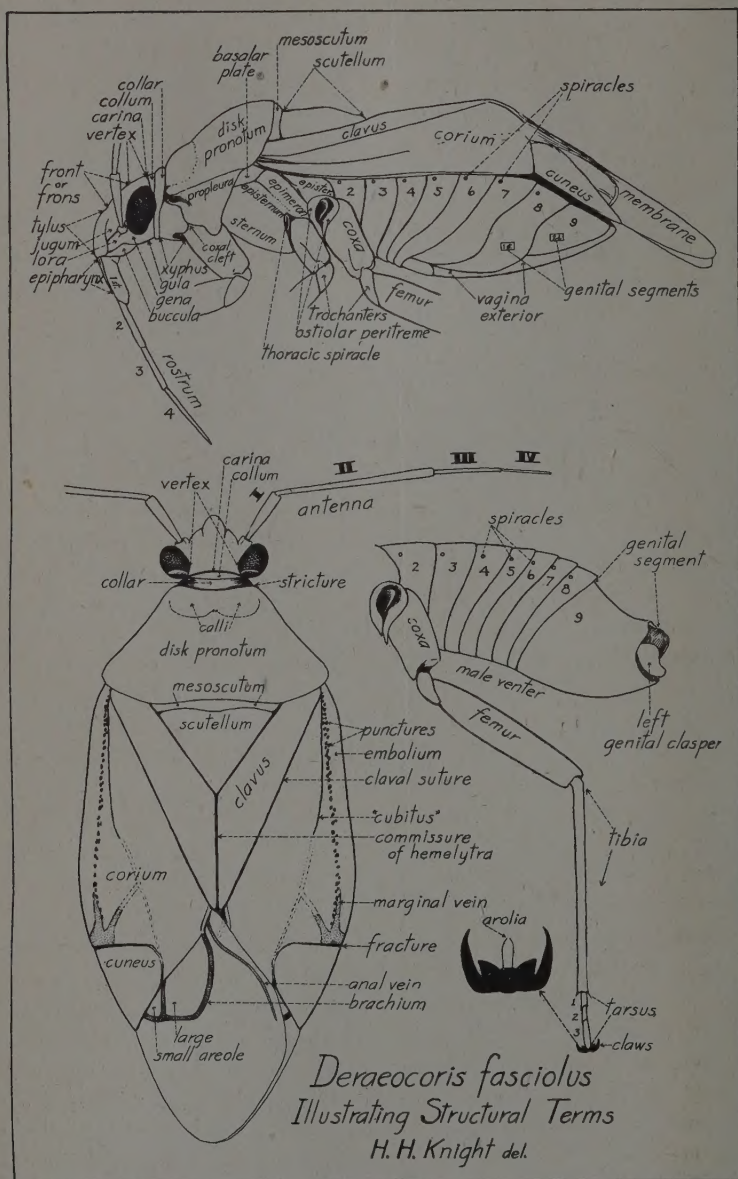*The University of Minnesota*
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UNIVERSITY FARM, ST. PAUL

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Deraeocoris fasciolus
Illustrating Structural Terms
H. H. Knight del.

Plate VIII

MONOGRAPH OF THE NORTH AMERICAN SPECIES OF DERAEOCORIS (HETEROPTERA, MIRIDAE)[1]

By Harry H. Knight

The genus Deraeocoris now includes all those species which have been described under Camptobrochis. Largely through the labors of Reuter and Poppius the genus is now known to have a world-wide distribution, ninety-three species and forty-three varieties being listed from parts other than the Nearctic region. In the present paper the writer has been able to recognize fifty-four species and twenty-two varieties from North America, of which *D. ruber* (Linn.) is common to both Nearctic and Palearctic regions, making a total of one hundred and forty-six species and sixty-two varieties from the world. Thirty-seven species and twenty varieties are herewith described as new.

Very little has been published regarding the life history and economy of these insects and in fact the species have been very imperfectly known. The writer has given special attention to the genus Deraeocoris during six seasons of collecting, and as a result, has been able to associate with definite host plants all but two of the known eastern species as well as certain of those found in the southwestern states. In several instances this relation appears to be more dependent on the predaceous habits of the bugs which feed largely on the aphids found on particular hosts, rather than the sap from the plant. In fact the writer has not detected a single case where the bugs have fed on the foliage of a plant and produced the characteristic leaf-bug injury which is always to be seen on plants infested by true leaf-feeders. The general scarcity of these insects as compared with leaf-feeding species is only another indication of their predatory habits, for predaceous forms never attain great abundance except sporadically in favored spots.

In the case of several species of Deraeocoris, if nymphs or adults are caged with succulent growth of the host plant, the bugs manage to live on sap alone but appear to prefer plant-lice or other small soft-bodied insects when such are available. Dr. W. H. Wellhouse has reared a specimen of *D. fasciolus* to the adult stage, the bug feeding only on the foliage of Crataegus, altho he found in rearing other specimens that aphids were fed upon when obtainable. The writer has found that *Deraeocoris aphidiphagus* feeds on *Schizoneura americana* Riley, while *D. nitenatus* feeds upon *Schizoneura lanigera* (of

Patch) on the elm; *D. fasciolus* feeds on *Aphis sorbi* Kaltenbach of the apple, upon *Schizoneura crataegi* Oestlund on Crataegus, and upon *Phyllaphis fagi* (Linn.) of the beech. These species are perhaps the best known, but others present equally interesting biological aspects. Several of the species live on conifers where they appear to be associated with aphids and other small soft-bodied insects which infest such trees. *D. pinicola* feeds at least in part on the pine-bark aphid, *Chermes pinicorticis* Fitch, while *D. nubilus* occurs on the same tree and most probably has similar habits. *D. laricicola* apparently breeds only on larch, *Larix laricina,* and when caged on succulent growth was found to feed on sap of the plant, altho it may well be predaceous in part, when opportunity permits, as is true of several species in the genus.

The nymphs of Deraeocoris present at least two characteristic forms. One group comprises several species in which the nymphs are typically covered with a white, powdery, flocculent material, and are thus in the early instars, not readily distinguished from the aphids among which they live. Nymphs of a second group, represented by *D. albigulus, nigritulus, pilosus,* and related species, are distinctly hairy and not covered with the white powdery substance as the above mentioned forms. The first group is composed of species which are known to be largely predaceous while the second group may prove to be forms which are primarily phytophagous.

The life histories of the species present some interesting variations. The *nebulosus* group, or subgenus Camptobrochis, comprising most of the species with punctate scutellum, contains forms that are known to pass the winter in hibernation as adults. The species of this group which have most frequently been taken in hibernation are *D. nebulosus, nubilus,* and *cuneatus.* Such a cycle is not the mode of life tor *D. grandis, aphidiphagus, betulae, pinicola,* and several other closely related species, for the writer has closely observed the disappearance of these insects at the end of their season and no pinned specimens have been noted which would indicate the contrary. Just how and where the eggs are laid are facts still awaiting investigation but the writer has repeatedly found the young nymphs of *D. aphidiphagus* in the curled elm leaves very soon after the leaf is rolled by the aphid *Schizoneura americana* Riley. The eggs are doubtless inserted in the buds or twigs of the tree and upon hatching the young nymphs probably travel about seeking until they find leaves which are infested by the aphids.

For the loan of material the writer is indebted to the authorities

of the United States National Museum, especially to Mr. E. H. Gibson and his assistant, Miss Emma Wells, who assembled all the Deraeocoris material from the collections contained there, including the Uhler types; to Dr. J. Chester Bradley for placing at the writer's disposal all the material in the Cornell University collection and the Heidemann collection now contained there; to Mr. E. P. Van Duzee for considerable material from the western states; to Mr. H. G. Barber, Dr. H. M. Parshley, Mr. Wm. T. Davis, Mr. J. R. de la Torre-Bueno, Mr. Chris. E. Olsen, Mr. W. L. McAtee, Dr. W. E. Britton, Prof. C. P. Gillette, Prof. C. J. Drake, Mr. W. J. Gerhard, Mrs. A. T. Slosson, Dr. C. P. Alexander for material from the Illinois Natural History Survey, and Dr. J. McDunnough for Canadian material. To these and to several other friends who have from time to time sent a few specimens, the writer wishes to express acknowledgment and appreciation.

Genus DERAEOCORIS Kirschbaum

Kirschbaum, 1855, Jahr. ver. Nat. Herz. Nassau, x, pp. 191, 208; (Sep.) Rhyn. v. Wiesb., Caps., pp. 31, 48. *Capsus* (*Deraeocoris*)

Stål, 1865, Hemip. Afr., iii, p. 20.

Stål, 1868, Hemip. Fabr., i, p. 87.

Reuter, 1875, Bihang Kongl. Sv. Vet.-Akad. Handl. iii, p. 21.

Reuter, 1875, Rev. Crit. Caps., [i] p. 84; [ii] p. 71.—Acta Soc. Fauna Fl. Fenn., i, p. 87.

Atkinson., 1890, Cat. Capsidae, p. 98.

Reuter, 1896, Hem. Gymn. Eur., v, pp. 18, 348.

Hüeber, 1902, Jahr. ver. Nat. Württ., 1902, p. 86; (Sep.) Synop. deut. Blindw., I, p. 378.

Distant, 1904, Fauna Brit. Ind., Rhyn., ii, p. 465.

Kirkaldy, 1906, Trans. Am. Ent. Soc., xxxii, p. 141.

Oshanin, 1909, Verz. Palae. Hemip., i, p. 748.

Oshanin, 1912, Kat. Palae. Hemip., p. 67.

Poppius, 1912, Acta Soc. Sci. Fenn., xli, No. 3, p. 118.

Van Duzee, 1916, Univ. Cal. Publ., Div. Ent. Tech. Bul., i, p. 209.

Van Duzee, 1917, Cat. Hemip., p. 356.

†*Capsus* Fieber, 1858, Wien. Ent. Monats., ii, p. 307.
Fieber, 1861, Eur. Hemip., p. 248.
Douglas and Scott, 1865, Brit. Hemip., p. 441.
Thomson, 1871, Opusc. Ent., iv, p. 429. *Capsus* (*Capsus*)
Jensen-Haarup, 1912, Danmarks Fauna, xii, p. 232.

Camptobrochis Fieber, 1858, Wien. Ent. Monats., ii, p. 304.
Fieber, 1861, Eur. Hemip., p. 264.
Douglas and Scott, 1865, Brit. Hemip., p. 447.
Reuter, 1875, Bihang Kongl. Sv. Vet.-Akad, Handl., iii, p. 20.

Reuter, 1875, Rev. Crit. Caps., [i] p. 83; [ii] p. 68.—Acta Soc. Faun.
　　　Fl. Fenn., i, p. 84.

Provancher, 1887, Pet. Faune Ent. Can., iii, p. 115.

Atkinson, 1890, Cat. Capsidae, p. 95.

Saunders, 1892, Het. Brit. Isds., p. 258.

Reuter, 1896, Hem. Gymn. Eur., v, pp. 37, 348. .

Hüeber, 1901, Jahr. ver. Nat. Württ., 1901, p. 181; (Sep.) Synop. deut.
　　　Blindw., I, p. 369.

Distant, 1904, Fauna Brit. Ind., Rhyn., ii, p. 460.

Kirkaldy, 1906, Trans. Am. Ent. Soc. xxxii, p. 140.

Reuter, 1909, Acta Soc. Sci. Fenn., xxxvi, No. 2, p. 52.

Oshanin, 1909 Verz. Palae. Hemip., i, p. 745.

Oshanin, 1912, Kat. Palae. Hemip., p. 67.

Van Duzee, 1916, Univ. Cal. Publ., Div. Ent. Tech. Bul., i, p. 209.

Camptobrochys Fieber, 1860, Eur. Hemip., p. 64.

Walker, 1873, Cat. Het., vi, p. 42.

Van Duzee, 1917, Cat. Hemip., p. 353.

Capsus (*Camptobrochus*) Thomson, 1871, Opusc. Ent., iv, p. 427.

Callicapsus Reuter, 1876, Ofv. Kongl. Vet.-Akad. Forh., xxxvi, p. 75.
　　　(Haplotype *histrio* Reut.)

Atkinson, 1890, Cat. Capsidae, p. 97.

Kirkaldy, 1906, Trans. Am. Ent. Soc., xxxii, p. 140.

Euarmosus Reuter, 1876, Ofv. Kongl. Vet.-Akad. Forh., xxxvi, p. 76.
　　　(Haplotype *sayi* Reut.)

Atkinson, 1890, Cat. Capsidae, p. 103.

Kirkaldy, 1906, Trans. Am. Ent. Soc., xxxii, p. 141.

Macrocapsus Reuter, 1879, Ofv. Finska Vet.-Soc. Forh., xxi, p. 55. (Hap-
　　　lotype *brachialis* Stal.)

Reuter, 1880, Zool. Jahresbericht, i, p. 509.

Chilocrates Horvath, 1889, Természetrajzi Füzetek, xii, p. 39. (Haplo-
　　　type *lenzii* Horv.)

Atkinson, 1890, Cat. Capsidae, p. 182.

Plexaris Kirkaldy, 1902, Entomologist, xxxv, p. 282. (Haplotype *saturnides*
　　　Kirk.)

Shana Kirkaldy, 1902, Entomologist, xxxv, p. 315. (Haplotype *ravana*
　　　Kirk.)

Mycterocoris Uhler, 1904, Proc. U. S. Nat. Mus., xxvii, p. 358. (Haplotype
　　　cerachates Uhl.)

Camptobrochis (*Euarmosus*) Reuter, 1909, Acta Soc. Sci. Fenn., xxxvi
　　　No. 2, p. 52.

Camptobrochys (*Euarmosus*) Van Duzee, 1917, Cat. Hemip., p. 355.

Camptobrochys (*Callicapsus*) Van Duzee, 1917, Cat. Hemip., p. 354.

Camptobrochys (*Mycterocoris*) Van Duzee, 1917, Cat. Hemip., p. 355.

The genus Deraeocoris was founded by Kirschbaum in 1855 as
a subgenus of Capsus (Authors) to include two new species and

thirty-nine previously described forms. Reuter (1875) removed nearly all the species which had been included by Kirschbaum, making the genus practically coextensive with Capsus of Fieber (1861), the latter author having failed to recognize Deraeocoris in his important work on the European Hemiptera. Distant (1904) named *olivaceus* (Fabr.) as genotype, while Kirkaldy (1906) to be more exact, named *medius* Kirschbaum (=*olivaceus* Fabr.) as type of Deraeocoris. A pseudotype, *ruber* (Linn.), was named by Oshanin (1912).

Reuter (1909) in a revision of the Nearctic species under the genus Camptobrochis, in substance expressed the opinion that he was very doubtful if Camptobrochis Fieber and Deraeocoris Kirschbaum are to be separated. It remained for Poppius (1912) in his great work on the African Miridae to definitely place Camptobrochis as a synonym of Deraeocoris. This conclusion was reached after that author had made a careful study of collections from every quarter of the globe, material which represented no doubt the greatest amount ever assembled. Mr. Van Duzee (1916) has indicated that Camptobrochis and Deraeocoris may be separated by characters found in the antennae and lateral margins of the pronotum. The writer would state that in the present work the number of North American species has grown until every variation from the cylindrical to clavate type of antenna is represented, likewise the carinate and ecarinate form of pronotum, there being a gradation of both characters so that among a few forms it is quite impossible to decide on that basis, into which group the species should be classed. The final outcome has been that a new set of characters has been brought forward in an effort to separate the genus into groups as indicated below.

After a considerable period of research for available characters in Deraeocoris, the writer has been able to separate the species into groups, one of which represents Camptobrochis as a subgenus, if we may have such, but in a much more restricted sense than has been the usage in the past. The species closely related to the genotype of Camptobrochis are chiefly distinguished by the punctate scutellum, spined character of the hind tibiae, a rather distinctive type of left genital clasper, and perhaps by the fact that the species hibernate as adults. In the North American fauna the group now includes *nebulosus* Uhler and ten other closely related species. Perhaps some workers would consider Camptobrochis as a genus on the premises submitted, but judging by a comparative study of tibial characters as found in the

other genera of the subfamily Deraeocorinae, Camptobrochis would appear to be only a part of the large genus Deraeocoris.

In an effort to settle the question regarding the proper name to use for our Nearctic species the writer has made an extended study of the possibilities for generic characters. In this work the one most constant character which appears to be distinctive throughout the large genus Deraeocoris is the arrangement of the spines on the front tibiae. In following the tibial characters it became necessary to refer elsewhere two species which have been recognized as aberrant in the genus, and with their removal a more satisfactory diagnosis may be drawn for Deraeocoris.

The Tibial Comb

In making a survey for available characters in the Miridae the writer discovered an interesting structure in the form of a comb at the distal end of the front tibiae. To this the writer applies the name *tibial comb* for it is very similar to the comb-like structures well known on the legs of certain Hymenoptera. For the Miridae there appears to be no mention in the literature of such a structure on the tibia, the small size and inconspicuous nature of the comb doubtless accounting for this. The tibial comb lies at the distal end of the fore tibia and in the same plane as the anterior face, there being no differences between the sexes. The comb is composed of a single row of very fine, closely placed, translucent spine-like teeth, set on the very apical margin of the tibia, usually bounded dorsally by one or more thick dark colored spines and ventrally in the same manner, the exact number and arrangement being different for each genus within a related group (Pl. IX). The front tibia is always more or less flattened on the anterior face near apex and usually very distinctly sulcate, these modifications being well adapted for cleaning both rostrum and antennae. On a few occasions the writer has observed living bugs cleaning the rostrum and antennae by applying the front feet, one on each side of the member and combing from base toward apex; in such cleaning operations the tibial comb undoubtedly has an important function. The tibial comb is fully developed in all the fourth and fifth stage nymphs which have been examined. A cursory examination of species in other families indicates that the tibial comb is present in all the Heteroptera having well developed antennae. In certain species of Reduviidae the comb is situated somewhat before the apex of the tibia.
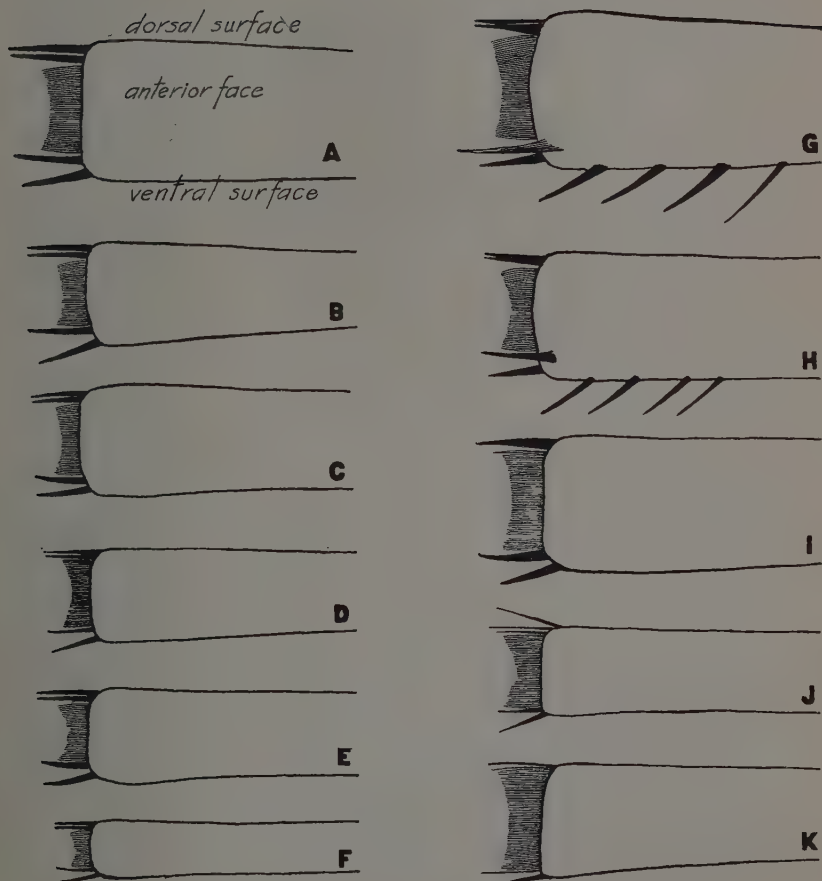
Plate IX. Illustrating the tibial comb and spines on the front tibiae of representative species of subfamily Deraeocorinae. A, *Deraeocoris olivaceus* Fabr.; B, *D. ruber* Linn.; C, *D. sayi* Reut.; D, *D. pinicola*; E. *D. grandis* Uhl.; F, *D. (Camptobrochis) nebulosus* Uhl.; G, *Deraeocapsus ingens* Van D.; H, *Deraeocapsus fraternus* Van D.; I, *Cimatlan grossum* Uhl.; J, *Eurychilopterella luridula* Reut.; K, *Diplozona collaris* Van D.

There appears to be little doubt that the spines, their form and arrangement on the tibiae, present characters which are correlated directly with a particular type of body structure, the combined elements of which are characteristic of small groups of species, or genera. Certainly the tibial spines are not specific in character but must pertain to a higher category. At present any statement regarding the general usefulness of tibial spines for distinguishing genera is of a preliminary nature, but in so far as the writer has carried his investigations it would appear that these characters will prove highly useful. In the Bryocorinae and Cylapinae the spineless character of the tibiae has been emphasized by Reuter, but to the writer it appears that the spines, their arrangement, or absence thereof, may be given more extended use, perhaps supplying additional and much needed criteria for distinguishing genera as well as certain larger groups within the family.

Subfamily DERAEOCORINAE

The writer would state the essential characters of the subfamily Deraeocorinae to be as follows:

Arolia very slender, bristle-like, erect, either parellel or only slightly curved, usually inclined slightly forward away from the tarsus, sometimes apparently absent or difficult to distinguish from the hairs on the tarsus, in the latter case the claws distinctly cleft; claws usually cleft but if not then the bristle-like arolia are distinct; pseudoarolia absent.

In a key to the subfamilies the writer (1918) raised the group Deraeocoraria Van D. (not Douglas and Scott) to the rank of a subfamily. This seems to be necessary if we are to have a logical and workable classification of the subfamilies based on characters found in the arolia. For a comparison of the structure and form of the arolia for the different subfamilies of Miridae the reader is referred to a plate of drawings by the writer (1918). Mr. Van Duzee (1916) sought to credit his division Deraeocoraria to Douglas and Scott (1865) but it seems to the writer that such a procedure is scarcely permissible in view of the fact that all the species which were included in the Deraeocoridae of Douglas and Scott are now known to belong in genera outside the group in question.

Of the genera known to the writer the following are placed in the subfamily Deraeocorinae: *Deraeocoris* Kirschb., *Klopicoris* Van D., *Diplozona* Van D., *Eurychilopterella* Reut., *Cimatlan* Dist., and

Deraeocapsus n. g. Other genera will doubtless be found to belong here when a careful study of the arolia is made throughout the family.

A diagnosis of the more essential characters of the genus Deraeocoris is as follows.

Body oval to suboval or more or less elongate, dorsum either glabrous or distinctly hairy, usually strongly shining, moderately or distinctly convex, distinctly punctate, head always and the scutellum in many species impunctate. *Head* usually broader than long, only rarely somewhat longer, very little depressed; basal carina usually distinct, in some species poorly defined or even absent, the vertex frequently indented just before the carina; collum frequently broadly exposed but exhibits transitions to forms where it is scarcely visible; front convex, smooth; tylus usually strongly protruding and well distinguished from the front; facial angle (when viewed from the side, the angle formed by the contour line of the tylus and the lower margin of the buccula) either a right angle or somewhat less; juga, lorae, and bucculae clearly defined, genae rather small, gula horizontal or only slightly depressed; eyes rather large and prominent, ovate when viewed from the side, nearly vertical or sloping slightly forward, posterior margins usually nearly parallel with the base of the head but in a few forms slightly removed. *Rostrum* reaching upon the middle coxae, only very rarely attaining hind margins of the posterior coxae, but exceptionally long in *grandis* where it reaches the second ventral segment; first segment usually attaining the base of head, very rarely longer. *Antennae* inserted slightly above the lower margin of the eye, pubescent to distinctly hairy; segment I of variable length, in some forms extending beyond tip of tylus by two-thirds its length; segment II of variable thickness, usually distinctly thickened toward apex, in the males frequently nearly cylindrical and about the thickness of or thicker than segment I, while in the females distinctly slender on the basal half and gradually enlarged toward apex. *Pronotum* trapezoidal, collar formed by a narrow ring-like apical constriction extending over the sides and beneath; disk moderately convex, broader at the base than long, gently sloping at the sides and immarginate, or distinctly margined and provided with a slender carina, the numerous species exhibiting gradual transitions from the marginate to the immarginate, margins usually nearly straight, but may be either slightly sulcate or arcuate; calli apparent as smooth shining ovals, flat or convex, frequently confluent and distinctly convex, in a few species very finely punctured; disk rather coarsely punctate except between the calli (rarely two punctures between) and on the subelevated area just before. *Scutellum* either punctate or impunctate, strongly convex or nearly flat. *Hemelytra* surpassing the tip of the abdomen, frequently more elongate in the males; cuneus rather strongly deflected, the fracture deep; membrane biareolate, smaller areole frequently much reduced, the brachium usually broadly curved to form the larger areole; membrane variously infuscated, frequently affording specific characters. Xyphus flat or slightly convex, margins bordering the coxal cavities carinate. *Legs* moderately long, the hind femora elongate, moderately incrassate, pubescent or distinctly hairy; tibiae beset with prominent hairs, the hind pair frequently with a row of spines on the anterior face, the middle pair sometimes with two rows of spines, front pair with distinct spines only at the apex; tibial comb terminated dorsally by two parallel spines of equal size, and ventrally by two spines

the second of which is slightly removed at base and divergent apically (Pl. IX). Hind tarsus with first segment shorter to slightly longer than the second, sometimes slightly thicker than the second but never twice as thick. Claws distinctly cleft near base, or more slender and without a distinct notch; arolia very slender, bristle-like, erect and parallel or only slightly curved at tips, in the smaller species sometimes difficult to distinguish from the hairs on tarsus. Structure of the male genital claspers giving specific differences.
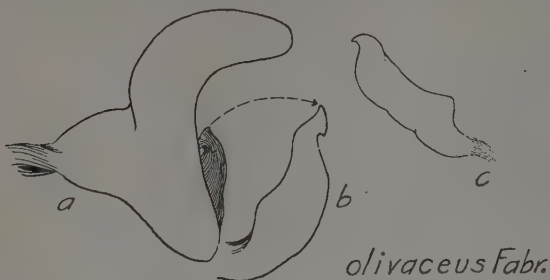
Fig. 1. *Deraeocoris olivaceus* Fabr., male genital claspers a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

METHODS OF STUDY

In this work exact measurements are given for structures of the insect which are commonly compared, one part with another, or measurements which in the writer's opinion are likely to be of value to future workers in the group. By following this plan it is feasible for a future student to make any comparison of structures he may so desire. Much has been said about the relative value of the various methods of comparing one structure with another where width and length are the factors involved, but it seems to the writer that the surest plan for meeting all the comparisons that the future student may require is to give all measurements in millimeters. This method need not preclude calling attention to the fact that the second antennal segment may be twice the length of the third, but when in addition, exact measurements are given for all the segments, the future student will also be in a position to compare the third or fourth segment with the first member, or with other parts as the need arises.

An explanation of the more important terms is as follows:

Length of the insect is the measurement taken between the tip of the tylus and the apex of the membrane; *width* is taken at the widest point on the hemelytra.

Head: *Width* is measured from the dorsal aspect and taken across the eyes at the widest point; *vertex* is the space between the inner margins of the eyes at the top of the head; *length* is measured laterally, taken at right angles to the base of the head, a point determined by the base of the gula and the hind margin of the eye.

Antenna: *Length* of the first segment is taken from the point of greatest constriction just above the basal knob, to the apex; the length of all the segments is taken when each is horizontal and extended straight to its full length.

Pronotum: *Length* is the greatest measurement that can be obtained along the median line, between the front margin of the collar and the hind margin of the disk, taken when the disk is turned as nearly horizontal as possible; *width* at base is taken across the basal angles of the disk; *width at anterior angles* is taken at the point where the front margins of the disk turn sharply inward to the constriction; *width of collar* is measured when viewed from the dorsal aspect.

The male genital claspers are shown in the present paper to be excellent characters for separating the species of Deraeocoris. For purposes of study and in order to make drawings of the genital claspers, the specimens should be placed in a moist chamber for a few hours. When sufficiently soft the tip of the abdomen may be picked off with the aid of two needles sharpened like chisels, working beneath the binocular microscope. The claspers may then be carefully separated from the attaching muscles and mounted for study. To make drawings the claspers should be removed to a dish coated with a mixture of paraffin and beeswax. This material makes an excellent surface for the manipulation of the claspers and for holding them in any desired position. The depth of the dish should be about one inch in order to guard against the claspers springing out when accidentally stressed by the point of the manipulating needle. Later the claspers may be removed on the point of a needle and attached with glue to a triangle mounted on the pin beneath the insect. At any future time the claspers may be studied as mounted on the pin, but if a change in position is required the claspers may easily be removed by placing the point in a watch glass containing water, and when the glue is dissolved remove to the paraffin dish as before.

The genital claspers figured in the present paper are all drawn to the same scale and turned to the same relative position for purposes of comparison. The figures were made by working with an eyepiece micrometer in the binocular microscope, a method by measurement which has proved more satisfactory than using the camera lucida.

The use of an eyepiece micrometer in the binocular microscope is a most valuable asset to the systematic worker, for by means of it a comparison between various parts of the insect may be made with the greatest speed and accuracy. For purposes of description the writer has found it a great saving of time to have worked out on a

card the equivalent in millimeters of all the micrometer readings from 1 to 100. Thus by a glance at the table one may read off in millimeters any micrometer measurement. Such a table is easily worked out by taking micrometer measurements on a standard millimeter rule which reads at least in tenths of a millimeter. Repeated measurements should be taken to ascertain the exact number of millimeters represented in say forty or fifty of the micrometer divisions, then by dividing one can find the length of a single micrometer division in thousandths of a millimeter. By a series of multiplications the table may be prepared and thus save future computations of this nature.
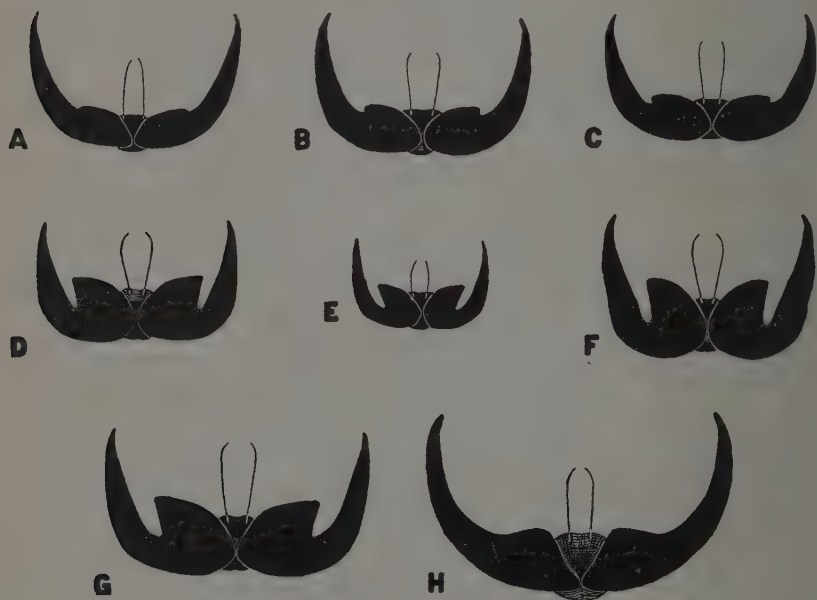
Fig. 2. Claws and arolia of representative species of Deraeocoris and Deraeocapsus. A, *Deraeocoris atriventris;* B, *D. pinicola;* C, *D. nigritulus;* D, *D. sayi;* E. *D. nebulosus;* F, *D. ruber;* G, *D. olivaceus;* H, *Deraeocapsus ingens.*

KEY TO THE GROUPS OF NORTH AMERICAN SPECIES OF DERAEOCORIS

1. Claws deeply cleft near base (fig. 2, D-G.)   2
    Claws not cleft or with only a slight indication (fig. 2, A-C)   .   .   7
2. Scutellum punctate   3
    Scutellum impunctate   5

Deraeocoris. There is a general similarity between the claspers of all the species and the differences are minute as compared with those found in the other groups of the genus. The right clasper is relatively small, yet careful comparison between the species has shown that slight but constant differences exist.

1. Dorsum bright red, clavus, a pair of large spots on corium and on pronotum black   .   .   .   .   .   . *histrio* Reuter p. 100
   Dorsum not red and black as the above   2
2. Cuneus red or stained with reddish; membrane hyaline or with only a fuscous spot at apex, or a point each side of middle   .   .   . 3
   Cuneus infuscated or with blackish, rarely reddish, but if so then the membrane distinctly blackish; membrane usually heavily marked with fuscous but if not then the cuneus without a trace of reddish   . 5
3. Segment II of the antennae not equal to length of pronotum; two fuscous spots on apical half of membrane, darkest specimens developing a brownish cloud distad of the spots   .   . *ornatus* n. sp. p. 99
   Segment II of antennae equal at least to length of pronotum, or longer; membrane hyaline or with an oval-shaped fuscous spot at apex   . 4
4. Membrane infuscated at apex; cuneus red, calli and scutellum fuscous to black   .   .   .   . *cuneatus* n.n. (=||*cunealis* Reut.) p. 96
   Membrane hyaline; cuneus, calli and scutellum reddish   .   .   .
   .   .   .   . *tinctus* n. sp. p. 95
5. Membrane nearly clear but having two small fuscous points, one at each side on the apical half   .   .   .   . *nebulosus* Uhler p. 91
   Membrane either hyaline or with fuscous but not marked as the above   6
6. Membrane with apical half hyaline or nearly so, not distinctly marked with fuscous; dorsum uniformly black   .   . *bakeri* n. sp. p. 102
   Membrane with the apical half infuscated, if not distinctly so then the dorsum more or less pallid gray   7
7. Dorsum uniformly black, sometimes narrowly pale at base of emboilum and corium; disk of pronotum never broadly pale or sordid gray at the sides   .   .   .   .   .   . *brevis* Uhler p. 103
   Dorsum not uniformly black, more or less sordid or pallid gray and marked with fuscous or black   8
8. Frons black, palest forms with a pale spot on median line at vertex but never extending upon frons; juga always black; median line of disk pale or at least palely indicated; distinctly ovate, hemelytra of male short, similar to the female   .   . *nigrifrons* n. sp. p. 108
   Frons with median line pale, or at least palely indicated, rarely black but in such case the disk of pronotum black and only the lateral margins pale; juga may be black but in such case the median line of disk is also black; females ovate, hemelytra of males distinctly elongate   9
9. Juga black, or slightly brownish in pale forms; disk of pronotum with black color always confluent over the median line   .   .   .   .
   .   .   .   . *brevis piceatus* n. var. p. 105.
   Juga pale, or at least brownish; pronotum grayish testaceous or with blackish, in the latter case the median line of the disk pale   .   . 10

Deraeocoris (Camptobrochis) nebulosus Uhler

1872 *Camptobrochis nebulosus* Uhler, U. S. Geol. Serv. Terr., Montana, Prelim.
        rept., p. 417.
1876 *Camptobrochis nebulosus* Uhler, Bul. U. S. Geol. Serv., i, p. 319.
1887 *Camptobrochis nebulosus* Provancher, Pet. Faune Ent. Can., iii, p. 116.
1878 *Camptobrochis nebulosus* Uhler, Proc. Bost. Soc. Nat. Hist., xix, p. 408.
1894 *Camptobrochis nebulosus* Uhler, Proc. Calif. Acad. Sci., ser. 2, iv, p. 265.
1894 *Camptobrochis nebulosus* Van Duzee, Bul. Buf. Soc. Nat. Sci., v, p. 178.
1895 *Camptobrochis nebulosus* Uhler, *in* Gillette and Baker, Hemip. Colo., p. 38.
1909 *Camptobrochis nebulosus* Reuter, Acta Soc. Sci. Fenn. xxxvi, No. 2. p. 59.
1916 *Camptobrochis nebulosus* Van Duzee, Check List Hemip., p. 41.
1917 *Camptobrochys nebulosus* Van Duzee, Cat. Hemip., p. 354.

Small, ovate, shining; olivaceo-testaceous and darkened with blackish, or
fuscous to blackish and marked with pale; membrane clear, a pair of small
fuscous points on the apical half, one each side of the middle.

♂. Length 3.5 mm. *Head*: width .97 mm., vertex .34 mm., length .4 mm.;
impunctate shining, carina prominent, sharply delimited behind but anteriorly
sloping gently to an impression on vertex; collum black, shining, broadly
exposed between carina and collar, a normal condition in this and related
species; black, carina broadly, juga and connecting line along base of tylus
with vitta on median line of frons, mark on tylus, bordering inner margin of
eyes and terminating in a spur on front margin of vertex, pale to olivaceo-
testaceous. *Rostrum,* length 1.22 mm., attaining middle of intermediate coxae,
piceous, slightly paler at the joints.

Antennae: segment I, length .25 mm., black, very finely pale pubescent; II,
1.17 mm., exceeding length of the pronotum, cylindrical, rather thick (.07 mm.),
constricted suddenly at base and apex, yellowish to brownish, apical one-fourth
and the base darkened, frequently the entire segment blackish, clothed with
fine short pale pubescence; III, .34 mm., slender, fuscous; IV, .34 mm., similar
to III only slightly more slender.
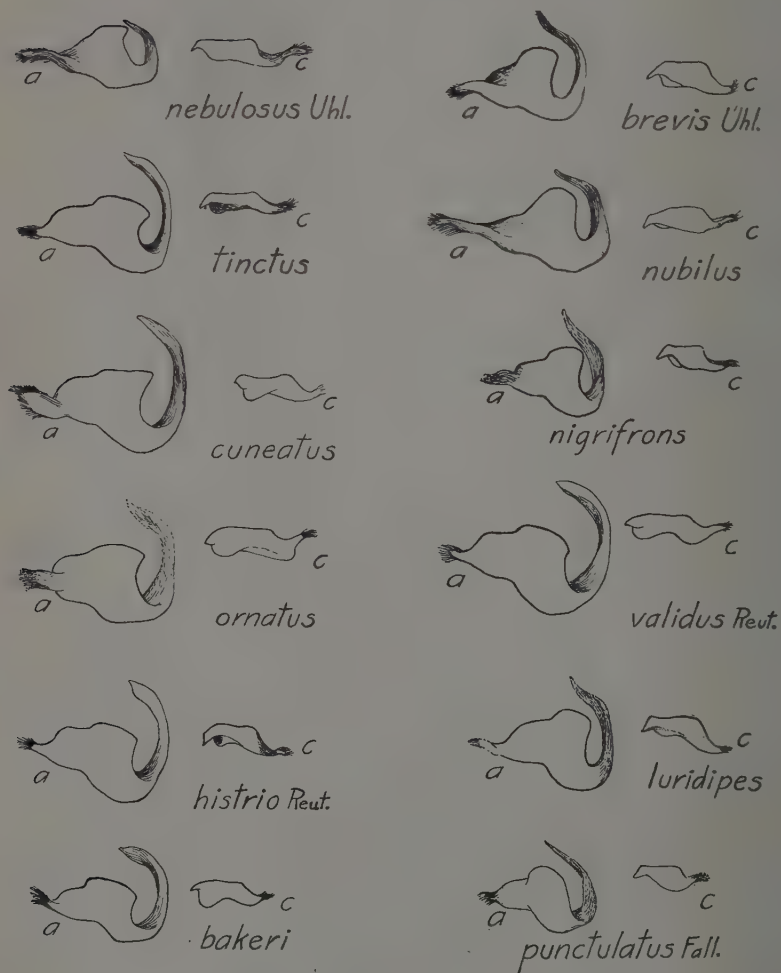
Plate X. Male genital claspers of the species of subgenus Camptobrochis; a, left clasper, lateral aspect; c, right clasper, lateral aspect.

Pronotum: length .91 mm., width at base 1.51 mm., anterior angles .71 mm., collar .54 mm.; disk moderately convex, lateral margins very slenderly carinate, slightly sulcate at middle, anterior angles distinct, posterior margin sinuate; calli flat, very slightly impressed and delimited behind by coarse punctures, black, seven to nine very fine punctures on the disk of each; collar slightly arcuate to the rear, yellowish; disk and pleural area coarsely but not densely punctate; disk olivaceo-testaceous, punctures always, a cloud of varying size each side of the median line and frequently upon the basal angles, fuscous to black; in darkest specimens only the slender basal margin, irregularly along median line, more or less between punctures posterior to outer margins of calli, testaceous; propleura black, lower margins pale, xyphus black, distinctly convex. *Scutellum* coarsely punctate, nearly flat, black, apex and lateral margins at base ivory-white; mesoscutum slightly exposed, black. *Sternum* and pleura black, ostiolar peritreme and usually the posterior and ventral margins of the epimera white.

Hemelytra: greatest width 1.74 mm., moderately convex, glabrous, shining, coarsely but not densely punctate, punctures black; testaceous, translucent, blackish color appearing first at apex of embolium and corium, then transversely across middle of corium and at base, and more or less broadly each side of the claval commissure; darkest specimens may be black except on base of embolium and clavus and a spot near base of corium. *Cuneus* nearly triangular, strongly deflexed, translucent on basal half, punctures and the apical half black. *Membrane* clear, the veins infuscated, more strongly posteriorly and invading the membrane slightly; two small fuscous points on the apical half, one each side of the middle, these spots being distinctive of the species.

Legs: coxae and femora black; femora shining, the apices yellowish brown, sometimes with an indistinct annulus just before, finely pale pubescent, a few fine long hairs on the antero-ventral surface; tibiae yellowish, slightly at knee, narrowly just below, more broadly at near middle, fuscous to blackish, the apices very slightly darkened; tibiae clothed with fine rather short pale pubescence, the anterior surface of middle and hind pair armed with a row of brownish spines, in length equal to thickness of the segment; tarsi testaceous, apical segment becoming blackish; claws deeply cleft, piceous; arolia minute, more slender than any hairs on tarsus, erect and subparallel, converging slightly apically (Fig. 2, E).

Venter: black, shining, finely pale pubescent; genital claspers distinctive of the species (Pl. X).

♀. Length 3.9 mm., width 1.94 mm., very similar to the male but slightly larger and more robust. Segment II, length .94 mm., slender on basal half, enlarged toward apex, the greatest thickness not equal to more than the diameter of segment I; yellowish to brownish, the apical one-fifth and less broadly at base, piceous, very finely pale pubescent.

Plesiotypes: ♂♀ July 18, Springfield, Missouri (H. H. Knight); author's collection. *Specimens examined*: ALABAMA,—♀ June 9, Auburn (H. H. Knight), tenerel condition. ARIZONA,—6♂♀ July 8—Aug. 6, Huachuca Mts., (H. G. Barber). COLORADO,—♂♀ July 28, Grand Junction. CONNECTICUT,—♀ Mar. 18, ♀ Aug. 6, New

Haven. ♀ Feb. 21, South Meriden (H. Johnson). ♀ Oct. 2, Westville. DISTRICT OF COLUMBIA,—May 9 to Oct. 20 (U. S. N. M.). ♂♀ Aug. 4, 1888 (Pergande). ♂ June 23, ♀ July 1, 3♂ 1♀ July 15, ♂ Aug. 18, ♀ Nov. 8, Washington (W. L. McAtee). FLORIDA, —♂ 2♀ Nov. 5-24, Monticello (H. B. Scammell). GEORGIA,— ♀ Sept., 1878 (C. V. Riley). ♂ July 31, Thomasville (C. S. Spooner). ♂ Aug. 6, Atlanta (J. C. Bradley). ILLINOIS,—♂♀ June 26 to Sept. 8, Urbana; ♂ June 13, Cobden; ♂ June 29, White Heath; ♀ July 6, Elizabeth; 3♂ ♀ Aug. 9, Du Bois; ♂♀ Aug. 18, Metropolis; ♀ Aug. 22, Meredosia (Ill. Nat. Hist. Survey). ♂ July 14, Chicago; ♂♀ Aug. 27, Gary; ♀ Sept. 18, Palos Park; ♀ July 16, Willow Springs (W. J. Gerhard). LOUISIANA,—♀ Sept. 15, Natchitoches. MARYLAND,— ♂♀ July 5, Great Falls, (O. Heidemann). ♂ July 26, Plummers Is. (W. L. McAtee). ♀ Aug. 6, Plummers Is. (R. C. Shannon). ♀ Aug. 5, Hagerstown. ♂ Sept. 25, Baltimore (P. R. Uhler). ♂ Feb. 9. Riverdale (W. W. Wallis). MASSACHUSETTS,—♂♀ Mar. 26 to Sept. 7, Northampton; ♂ May 14, Wellesley; ♀ 13 Aug., ♂♀ Sept. 2, Lynn; ♀ Sept. 7, Saugus; ♀ Sept. 24, ♀ Oct. 13, Boston (H. M. Parshley). 2♂ July 20, Sharon (E. P. Van Duzee). ♀ July 22, Auburndale; ♂♀ Sept. 3, Needham, (C. W. Johnson). MINNESOTA,—♂♀ July 8 to Oct. 9, St. Anthony Park (H. H. Knight), breeding on *Quercus macrocarpa.* MISSOURI,—♂♀, nymphs, July (C. V. Riley). ♂♀ May 30 to July 28, Charleston (E. H. Gibson). 12♂♀ July 18, Springfield; 12♂♀ July 22, Hollister (H. H. Knight), on young white oak. NEBRASKA,—♂ Aug. 10, Falls City (H. G. Barber). NORTH CAROLINA,—♂♀ April 4 to June 9, Southern Pines (A. H. Manee). ♂♀ June 1 to July 14, Black Mts. (Beutenmuller). ♂ Oct. Raleigh (J. E. Eckert). NEW HAMPSHIRE,—♂♀ Franconia; ♂♀ Mt. Washington (Mrs. A. T. Slosson). NEW JERSEY,—♂♀ July 27, Bear Swamp, Ramapo Mts. (H. G. Barber). ♀ Sept. 7, Fort Lee. NEW YORK, —♂♀ June 8 to Sept. 27, Batavia; ♂ July 27, McLean; ♂♀ Feb. 13 (under bark of log), 2♀ April 8 (under sycamore bark), 2♂ 4♀ July 26, ♂ Oct. 19 (in house), Ithaca (H. H. Knight). ♂♀ June 30 to July 27, White Plains (Torre-Bueno). ♀ July 24, Salamanca; ♀ June 13, Niagara Falls (E. P. Van Duzee). ♀ July 19, Cranberry Lake (H. Osborn). ♀ Aug. 27, Schenectady, (O. Heidemann). ♂ Aug. 1, Maspeth; ♀ Aug. 24, Rockaway Beach; ♀ Sept., Port Washington; 2♂ July 23, Staten Is. (C. E. Olson). ♀ July 9, Staten Is.; ♀ Sept., Yaphank; ♂ Oct. 9, Brooklyn; ♀ May 26, Rockaway Beach (Wm. T. Davis). ♂♀ July 30, Cold Spring Harbor, ♀ Aug. 3, West Point (H. G. Barber). OHIO,—♀ Sept. 2, Vermillion (E. P. Van Duzee).

PENNSYLVANIA,—♀ May 25, Philadelphia. ♂♀ Nov. 23, Harrisburg. ♂♀ Delaware Watergap (Mrs. A. T. Slosson). ♂ July 22, Reading (W. J. Gerhard). TEXAS,—♀, September. VIRGINIA,— ♀ June 19, 1881 (P. R. Uhler). ♀ July 28, Fairfax Co. (R. C. Shannon). ♂ Aug. 23, Vienna (H. G. Barber). 2♂ ♀ Aug. 28, Pulaski (Torre-Bueno). ONTARIO, CANADA,—2♀, Grimsby (Petit). ♂♀ June 22, Norway Point, Lake of Bays (J. McDunnough). ♀ Aug. 18, Ottawa (G. Beaulieu).

This species has been frequently taken in hibernation, under bark and in buildings. In Missouri the writer found it numerous on young white oak and more recently, in Minnesota, the nymphs and adults were found abundant the latter part of July on *Quercus macrocarpa*. The majority of the nymphs mature the latter part of July and the adults are most abundant on the trees in early August. On October 6 and again October 9 a living specimen of *nebulosus* appeared on the writer's table in the laboratory while he was working up data on this very form. The specimens came no doubt from the bur oaks on the campus where the species bred abundantly, later entering the building for hibernation. The species has been taken singly on various plants; also it is frequently attracted to lights.

Specimens taken August 4, 1888, by Pergande are labeled "on oak." Specimens from Miss Murfeldt and now in the U. S. N. M. collection, bear the label: "Predatory bug, on *Ph. Rileyi*, Sept. 2, 1889." This evidently refers to *Phylloxera rileyi* Riley of the oak, the same tree upon which *nebulosus* is most frequently found.

The type locality for this species is not given in the original description, but the specimens probably came from Colorado as was the case with several other species described in the same paper. The type specimens are not to be found, or at least were not recognized, in the material of the National Museum collection.

Deraeocoris (Camptobrochis) tinctus new species

Slightly larger than *nebulosus*, structurally and in general aspect rather intermediate between *cuneatus* and *nebulosus*; testaceous or pale brownish, stained with reddish, punctures black, hemelytra somewhat translucent, membrane clear or only slightly brownish bordering the brachium; structurally as in *nebulosus* unless otherwise noted.

♂. Length 4 mm. *Head*: width .97 mm., vertex .41 mm., length .43 mm.; pale to brownish, the areas represented by black in *nebulosus* are replaced chiefly by brown in this species; collum pitchy black, spot each side of vertex, sides of tylus, genae, juga and bucculae, more or less blackish. *Rostrum*, length 1.37 mm., attaining middle of intermediate coxae, blackish, paler at the joints.

Antennae: segment I, length .3 mm., brownish to blackish, becoming darker first at base and apex; II, 1.05 mm., equal to length of pronotum, greatest thickness .08 mm., brownish black, usually paler on the middle one-third; segments III and IV missing.

Pronotum: length 1.05 mm., width at base 1.71 mm., anterior angles .8 mm., collar .63 mm.; more finely and sparsely punctured than in *nebulosus;* disk rather uniformly testaceous or pale brownish, calli reddish brown, sometimes becoming blackish around the margins, disk of each callus with two or three very fine punctures; propleura testaceous, paler below, surrounding base of coxal cleft and the stricture above black, collar pale; xyphus slightly convex, blackish, rather longly pale pubescent. *Scutellum* punctate, reddish brown, punctures black, lateral margins and apex white, median line pale, frequently indistinct; frenal margin and the suture separating the mesoscutum black; mesoscutum scarcely exposed, brownish, sutures black. *Sternum* and pleura brownish black, basalar plate, posterior and ventral margins of epimera, more or less pale; ostiolar peritreme white.

Hemelytra: width 1.91 mm., glabrous, pale yellowish, translucent, slightly reddish at apex of embolium; punctures moderately fine, uniformly distributed, black. *Cuneus* reddish translucent, outer margin paler, punctures very fine or absent. *Membrane* clear, brachium brownish at apical margin of cells, frequently the membrane slightly stained at apex of larger areole.

Legs: coxae fuscous to black, paler at apices; trochanters and femora testaceous to reddish brown, translucent, apical half usually more reddish, apex pale, frequently a subapical band is also apparent, presenting a reddish annulus dividing the pale; tibiae pale, banded as in *nebulosus* except that the black is replaced by reddish brown, the knees becoming piceous and the apical band fuscous; tarsi fusco-brownish, becoming blackish on the apical segment.

Venter: reddish to fusco-brownish and piceous, finely pale pubescent; genital claspers (Pl. X) distinctive of the species.

♀. Length 4.4 mm., width 2.1 mm.; very similar to the male but slightly larger; segment II, length 1.05 mm., slender, slightly thickened toward apex, piceous to black, the middle one-third pale to reddish brown.

Holotype: ♂ July 28, Grand Junction, Colorado; Cornell University collection. *Allotype*: same data as the type. *Paratypes*: 5♂ 4♀, topotypic. ♀ May 27, Delta, Colorado.

Deraeocoris (Camptobrochis) cuneatus new name

1909 *Camptobrochis validus* var. *cunealis* Reuter, Acta Soc. Sci. Fenn., xxxvi, No. 2, p. 59. (name preoccupied)
1916 *Camptobrochis validus* var. *cunealis* Van Duzee, Check List Hemip. p. 41.
1917 *Camptobrochys validus* var. *cunealis* Van Duzee, Cat. Hemip., p. 354.
1919 *Camptobrochis poecilus* (Reuter MS) McAtee, Ent. News xxx, p. 246.

Slightly larger than but structurally very close to *nebulosus;* olivaceotestaceous to brownish and blackish, cuneus red, membrane clear, a rather distinct somewhat oval-shaped fuscous spot on the apex.

♂. Length 4.2 mm. *Head*: width .92 mm., vertex .37 mm., length .43 mm.; structurally and in color markings very similar to *nebulosus,* the pale color

more broadly developed, bases of genae and lorae, narrow tip of tylus and lower margin of bucculae, yellowish, eyes brown to blackish; genae longly pale pubescent. *Rostrum,* length 1.48 mm., just reaching upon the intermediate coxae, brownish to piceous, paler at the joints.

Antennae: segment I, length .37 mm., black, shining, slightly pale at extreme tip; II, 1.2 mm., cylindrical as in *nebulosus* (.08 mm. thick), black, pale pubescent; III, .43 mm.; IV, .48 mm.; the last two segments black, pale pubescent, a few hairs equal to twice the thickness of segment.

Pronotum: length 1.08 mm., width at base 1.8 mm., anterior angles .83 mm.; nearly as in *nebulosus,* lateral carina and anterior angles more distinct, anterior margin distinctly sulcate at termination of anterior angles; calli very slightly convex, black, five to seven punctures on disk of each; disk more or less brownish, narrow basal margin, lateral carina, median line, just before calli, more or less just posterior to outer angles of calli, pale to testaceous; propleura brownish black, lower margin, anterior margin of xyphus and the collar, pale to yellowish. *Scutellum* punctate, brownish black, apex and lateral margins basally ivory-white, the median line palely indicated. *Sternum* and pleura black, basalar plate, posterior and ventral margins of epimera brownish; ostiolar peritreme white.

Hemelytra: width 2 mm., translucent yellowish brown, punctures black; becoming dark brownish or piceous on disk of corium, tip of embolium, rather broadly along claval commissure and narrow margin bordering scutellum. *Cuneus* bright red, sometimes brownish at apex and narrowly testaceous at base. *Membrane* pale, veins infuscated, infuscation invading the membrane slightly at posterior margin of areoles; distal one-third occupied by a rather distinct oval-shaped pale fuscous spot, the infuscation usually not attaining the margin.

Legs: reddish brown to piceous or black, trochanters and apices of coxae testaceous; apices of femora pale, usually with an indistinct annulus just before apex; tibiae pale or yellowish, knees, narrow band just below and sometimes connected dorsally with spot on knee, a broader band just short of middle, band at apex altho in paler specimens nearly obsolete, dark brownish to piceous, bands on anterior tibiae less distinct; tarsi testaceous, becoming blackish at apex; pubescence, spines, and claws similar to *nebulosus;* in the reddish or pale specimens the piceous coloration may appear in spots on anterior face of femora.

Venter: dark reddish to piceous or black, shining, finely pale pubescent; genital claspers (Pl. X) distinctive of the species.

♀. Length 4.9 mm., width 2.4 mm.; very similar to the male but slightly more robust; segment II, length 1.2 mm., just equal to length of the pronotum, slender as in the female of *nebulosus,* slightly enlarged toward apex, piceous, the middle one-third yellowish or brownish.

Plesiotypes: ♂ May 21, Orange, Conn. (A. B. Champlain); ♀ June 6, Brown's Ferry, Savannah river, South Carolina (H. H. Knight); author's collection. *Specimens examined*: CONNECTI-CUT,—♀ May 15, Portland (B. H. Walden), on *Pinus strobus.* ♀ May 15, New Haven (A. B. Champlain). DISTRICT OF COLUMBIA, —♂ April 21, ♀ July 10, 1885; ♀ June 20, 1888, ♀ June 20, 1893, ♀ July 20, Washington (O. Heidemann). ♀ May 20, (D. C. Clemons).

ILLINOIS,—2♂, ♀ Aug., 1889, Quincy (C. A. Hart).   ♀ June 14, Carmi.   ♀ June 24, Grand Tower.   MARYLAND,—♀ Feb. 1, Little Falls, under sycamore bark; ♂♀ Mar. 1, East Riverdale (W. L. Mc-Atee), under birch bark.   ♂ Aug. 22, Blandensburg; ♂ Aug. 29, Forest Glen (H. G. Barber).   ♂ July 8, 1893, Glen Echo; ♀ Aug. 10, 1890, Blandensburg (O. Heidemann). MASSACHUSETTS,—♀ April 6, Forest Hills (C. L. Mason).   ♀ Aug. 8, Chester (C. W. Johnson). NEW JERSEY,—♂♀ Oct. 3, Roselle Park; ♀ Oct. 15, Madison (H. G. Barber).   NORTH CAROLINA,—♂♀ July 15, Swannanoa, alt. 3,000 ft. (R. W. Leiby).   NEW HAMPSHIRE,—♂♀ Mt. Washington (Mrs. A. T. Slosson).   NEW YORK,—♀ July 24, on *Pinus strobus,* ♀ July 26, Ithaca; ♀ July 27, McLean (H. H. Knight).   PENN-SYLVANIA,—♂ 3♀ Delaware Watergap (Mrs. A. T. Slosson). SOUTH CAROLINA,—♀ June 6, Brown's Ferry, Savannah River (H. H. Knight), taken on *Alnus rugosa.*   WEST VIRGINIA,—♀ July 25, 1887, Berkeley Springs (O. Heidemann).

This species was described by Reuter as a variety of *validus* but it proves on close examination to be a distinct species. It may be distinguished by the well defined and punctate calli, the rich brownish color with red cuneus, more or less oval-shaped fuscous spot at apex of membrane, and by the structure of the genital claspers (Pl. X). *Cuneatus* is more robust than *nubilus,* particularly the males, which have shorter hemelytra in proportion to the body, being more like the females in form.

Mr. McAtee found this species developing on *Alnus rugosa* which is probably the preferred host plant. In New York the writer took a teneral specimen on *Pinus strobus* which had undoubtedly developed on that tree, and the species has also been collected on the same tree in Connecticut. Judging by the habits of related species, the writer would not be surprised to learn that *cuneatus* is predaceous upon the alder blight aphid, *Pemphigus tessellatus* Fitch, and the pine bark aphid, *Chermes pinicorticis* Fitch.

Reuter's chirotype for the manuscript name "*Camptobrochis poecilus*" is in the U. S. National Museum collection,—♂ Washington, D. C. (O. Heidemann). Uhler's manuscript name for the species was "*Camptobrochis crassicornis,*" three specimens having been noted with this label.

Deraeocoris (Camptobrochis) ornatus new species

Very similar to *cuneatus,* but segment II of the antennae is shorter in proportion to length of pronotum, also the punctures on the disk are finer; two rounded fuscous spots on apical half of membrane are suggestive of *nebulosus* but darkest specimens may develop a brownish cloud distad of the spots.

♂. Length 4.5 mm. *Head*: width 1.01 mm., vertex .4 mm., length .48 mm.; nearly as in *cuneatus,* the front less convex, reddish brown each side of median line; lorae, genae, bucculae, apical margin of tylus, and two impressed spots on vertex, black. *Rostrum,* length 1.48 mm., nearly as in *cuneatus.*

Antennae: segment I, length .34 mm., basal half reddish brown, piceous apically; II, 1.11 mm., scarcely equal to length of pronotum, thickness .085 mm., black, brown annulus indicated at middle; III, .4 mm.; IV, .4 mm.; last two segments black, pale pubescent as in *cuneatus.*

Pronotum: length 1.14 mm., width at base 1.92 mm., anterior angles .92 mm., collar .67 mm.; more finely punctate and the lateral margins of the disk more nearly straight than in *cuneatus;* calli black, reddish brown around the margin and extending more or less toward the anterior angles of disk; grayish testaceous, paler near margins of disk and at the median line, not so distinctly brownish as in *cuneatus. Scutellum* reddish brown or becoming piceous, punctures black, apex and lateral margins ivory-white, median line usually indicated; mesoscutum black, scarcely exposed. *Sternum* and pleura black, posterior and ventral margins of epimera brownish; ostiolar peritreme white.

Hemelytra: width 2.08 mm.; grayish translucent, punctures, frenal margin, more or less along commissure, spot at middle and along apical margin of corium, piceous, tip of embolium reddish translucent. *Cuneus* red, translucent, paler at inner angle and outer margin, slenderly piceous on inner margin near apex, several very fine black punctures evident. *Membrane* pale, brachium infuscated, more or less invading the membrane on both sides; a pair of rounded fuscous spots on the apical half, one each side of the middle, darkest specimens developing a brownish cloud distad of the spots.

Legs: coxae black, the apices and trochanters testaceous; femora reddish brown, piceous on the basal half, in darkest specimens only the apical one-third paler and annulated with reddish; tibiae nearly as in *cuneatus,* annulations dark reddish or piceous; tarsi brownish black, the two basal segments paler.

Venter: dark reddish to piceous and black, shining, pale yellowish pubescent; genital claspers (Pl. X) distinctive of the species.

♀. Length 4.8 mm., width 2.34 mm., very similar to the male; segment II, length 1.08 mm., slightly shorter than length of pronotum (1.2 mm.), black, the middle one-third testaceous or brownish, all the other segments black, pubescence as in *cuneatus.*

Holotype: ♂ Oct. 22, Yankton, South Dakota; author's collection. *Allotype*: topotypic. *Paratypes*: ILLINOIS,—♀, "Ill." (C. V. Riley). MISSOURI,—♂ July 12, Wittenburg. ♂♀ "Mo." (C. V. Riley). NEBRASKA,—♀ Aug. 28, Bigelow (H. G. Barber). SOUTH DAKOTA,—3♀, taken with the types.

Deraeocoris (Camptobrochis) histrio (Reuter)

1876 *Callicapsus histrio* Reuter, Ofv. Kongl. Sv. Vet.-Akad. Forh., xxxii, No. 9, p. 75.

1895 *Callicapsus histrio* Blatchley, Psyche, vii, p. 279.

1909 *Camptobrochis histrio* Reuter, Acta Soc. Sci. Fenn. xxxvi, No. 2, pp. 54, 58.

1917 *Camptobrochys (Callicapsus) histrio* Van Duzee, Cat. Hemip., p. 355.

♂. Length 4.6 mm. *Head*: width .91 mm., vertex .42 mm., length .48 mm.; carina present but low and broad, slightly impressed just before, collum broadly exposed as in other species of this group; black, carina, spot each side of vertex bordering the eye, slender ventral margin of bucculae and tylus, pale. *Rostrum*, length 1.85 mm., reaching to middle of hind coxae, piceous, somewhat paler on segment I.

Antennae: segment I, length .42 mm.; II, 1.2 mm., nearly cylindrical but slightly more slender toward the base, equal in thickness to segment I, pubescence pale to black, rather short and closely set, longest hairs not equal to thickness of the segment; III, .45 mm.; IV, .51 mm.; black, the last two segments slender, very finely pale pubescent, a few exserted hairs equal to thickness of the segment.

Pronotum: length 1.11 mm., width at base 1.85 mm., anterior angles .83 mm., collar .65 mm.; disk convex, lateral margins distinct, nearly straight, strongly narrowed anteriorly, coarsely and rather uniformly but not densely punctate; disk pale red to bright red, punctures becoming black, calli except at antero-lateral angles and a widening stripe behind each which falls short of the basal margin, black; calli moderately convex, three or four fine punctures on the disk of each, delimited behind by coarse punctures, a pair of deep punctures set between the callosities, one each side of the median line; propleura black, red dorsally, pale bordering the coxal cavities; xyphus moderately convex, black, paler at margins and including the collar in front, pale pubescent. *Scutellum* red, a black spot on median line at base, punctate, the punctures only slightly darkened. *Sternum* and pleura black; ostiolar peritreme black but usually with some pale points.

Hemelytra: width 2.2 mm., red (sometimes slightly pallid where the melanin pigment has not been fully oxidized to red), clavus except apex, triangle at base of corium, and a large somewhat rounded spot on the apical half black, punctures mostly blackish. *Cuneus* red, punctures concolorous, usually a blackish streak along inner margin near apex. *Membrane* dark fuscous, an irregular transverse band at middle pale, the apical half with a crescent-shaped fuscous cloud which does not always attain the margin.

Legs: black, shining; tibiae biannulate with pale, the front pair frequently with only one annulus; tarsi brownish black, darker at apex, claws brownish to piceous.

Venter: black, shining, finely pale pubescent; genital claspers (Pl. X) distinctive of the species.

♀. Length 5 mm., width 2.2 mm.; very similar to the male but usually slightly larger; segment II of antennae more slender on the basal half, tapering from base to larger at apex.

Plesiotypes: ♂♀ August 17, Langdon, Missouri (H. G. Barber); author's collection. *Specimens examined*: CALIFORNIA,—♂♀ Aug. 1, Lakeport, Lake Co. (E. P. Van Duzee); one specimen Marysville, Yuba County (*fide* Van Duzee). DISTRICT OF COLUMBIA,—♀ Nov. 24, 1886, ♀ Feb. 21, 1887 (T. Pergande). ♂ Nov. 4, 1887 (O. Heidemann). ILLINOIS,—♂♀ July 4 to July 31, 3♂ 1♀ Aug. 18, ♂ Aug. 23, ♂ Nov. 1, Chicago; ♀ Aug. 31, Argo; 2♂ Sept. 19, Palos Park (W. J. Gerhard). ♀ June 1, Grand Tower; ♂ June 14, Savanna (J. R. Malloch). ♂ June 8, 1890, ♂ June 17, 1887, "Ill." (C. A. Hart). INDIANA,—♂♀ July 14, Mineral Springs (A. B. Walcott). IOWA, —♂♀ "Ia." (U. S. N. M.). KANSAS,—♂ Onaga (Crevecoeur). ♀ June 19, ♂ July 13 (Popenoe); 2♂ Sept. 1, (J. B. Norton); ♂ Mar. 16, ♂ July 11, ♂ Sept. 23 (P. J. Parrott); ♀ June, Riley County (Marlatt). 2♂ June 28, Wellington. MICHIGAN,—♂ 2♀ July 3, Berrien County (R. F. Hussey). MINNESOTA,—♀, "Minn." (Lugger collection). MISSOURI,—♂ July 6, ♀ July 10, 2♂ 2♀ July 14, Langdon (H. G. Barber). 2♂ July 22, O'Fallon (W. L. McAtee). MONTANA,—♀ Aug. 21, 1892, Assinuaboin (Heidemann collection). NEBRASKA,—♀, "Neb." (Lugger collection). NEW YORK,—♂ Aug. 21, Ithaca. ♀ Aug. 30, Cold Spring Harbor, Long Island (H. M. Parshley). SOUTH DAKOTA,—2♀ Aug. 5, 2♂ Sept. 25, Ardmore (E. G. Holt).

This species has frequently been taken in hiberation as is shown by the above records. Mr. W. J. Gerhard found the species fairly abundant about electric lights in the suburbs of Chicago during July and August, 1914. Probably the majority of all specimens collected have been taken at lights or in hibernation. Nothing is known regarding the life history altho the general scarcity of specimens and the wide distribution of the species suggests that it is predaceous in habits. Blatchley (1895) records two specimens that "were found beneath the bark of a black oak log (*Quercus coccinea tinctoria* Gray) which lay on the side of a high sandy hill near the Wabash River. Feb. 19, 1893."

Reuter (1876) described *histrio* and erected the genus Callicapsus for its reception, recording the locality as "Texas" and "Carolina." The type specimens are probably still to be found in the Stockholm National Museum. In a later examination of the species, Reuter (1909) placed it in Camptobrochis, pointing out that structurally *histrio* differs very little from *punctulatus* Fallen and other closely related species.

Deraeocoris (Camptobrochis) bakeri new species

1909 †Camptobrochis brevis Reuter, Acta Soc. Sci. Fenn., xxxvi. No. 2, p. 59.

Black, shining, legs reddish brown; scarcely larger than *nebulosus,* anterior angles of pronotum broader and more prominent; apical half of membrane clear.

♂. Length 4.1 mm. *Head*: width .91 mm., vertex .45 mm., length .43 mm.; black, polished, carina ivory-white, apical half of tylus more or less and sometimes the median line of front pale or brownish; collum broadly exposed, front more convex than in *nebulosus. Rostrum,* length 1.35 mm., reaching upon middle of intermediate coxae, piceous, the two basal segments more brownish.

Antennae: segment I, length .31 mm.; II, .94 mm., nearly cylindrical, thickness .06 mm., slightly thicker on the apical half; III, .37 mm.; IV, .34 mm.; black, pale pubescent, the longer hairs slightly darkened.

Pronotum: length 1.03 mm., width at base 1.65 mm., anterior angles .86 mm., collar .6 mm.; black, disk broader and the anterior angles more prominent than in *nebulosus,* coarsely and closely punctate; calli confluent, forming a transverse convex polished area, usually with two or three fine punctures near the posterior lateral angles; collar white except just behind the eyes, as viewed from above distinctly arcuate to the rear; basal margin of disk very slenderly, lower pleural margins and xyphus except on disk, pale to white. *Scutellum* black, coarsely punctate, narrow apex and sometimes the lateral margins very slenderly pale. *Sterum* and pleura black, posterior and ventral margins of epimera pale; ostiolar peritreme white.

Hemelytra: width 1.72 mm.; black, closely punctate, more coarsely on clavus near scutellum; glabrous or only minutely and sparsely pubescent on embolium. *Cuneus* black, distinctly punctured. *Membrane* clear, veins and apical half of areoles infuscated, the infuscation invading the membrane narrowly just posterior to the brachium.

Legs: testaceous to reddish brown, coxae fuscous to black; basal half of femora frequently piceous, the apical half not distinctly banded; tibiae reddish brown, usually banded with darker at middle and apex, the knee and a line just below on dorsal side reddish to piceous; tarsi infuscated, becoming black toward apex, claws piceous.

Venter: dark reddish brown to piceous and black, shining, pale pubescent; genital claspers (Pl. X) distinctive of the species.

♀. Length 4.3 mm., width 2.08 mm., very similar to the male but more robust; segment II, length 1 mm., slender, gradually thickened toward apex (.057 mm. thick); all the segments black, pale pubescent, beset with several long pale or slightly darkened hairs.

Holotype: ♀ July, Ormsby County, Nevada (C. F. Baker) author's collection. *Allotype*: topotypic; Cornell University collection *Paratypes*: NEVADA,—2♂ July 6, Ormsby County (C. F. Baker) ♀ Virginia City; ♀ "76." (Uhler collection). CALIFORNIA,—♂ Aug 24, Donner Lake, Placer Co. (W. M. Giffard). ♀ July 10, Lake Taho UTAH,—♂ Sept. 18, Milford (J. C. Bradley). COLORADO,—♂ July 25, Rifle; ♀ May 27, Delta.

Uhler did not separate this species from his *brevis* as is shown by determination labels on specimens. Reuter (1909) had this species before him when discussing *brevis*, a fact easily ascertained from that author's remarks as well as a determined specimen in the Heidemann collection. Uhler's description of *brevis* was misleading in that he described the membrane as "soiled white," a term more applicable to the species here described.

Deraeocoris (Camptobrochis) brevis (Uhler)

1904 *Camptobrochis brevis* Uhler, Proc. U. S. Natl. Mus., xxvii, p. 359.
1917 *Camptobrochys brevis* Van Duzee, Cat. Hemip., p. 354.

Piceous to black, shining, larger and more elongate than *nebulosus;* membrane infuscated near the apex.

♂. Length 4.7 mm. *Head*: width .97 mm., vertex .4 mm., length .48 mm.; black, shining, the carina, spot near front margin of eye and a more obscure mark on median line of frons, yellowish to ivory-white, eyes brownish to black. *Rostrum,* length 1.54 mm., attaining the middle of the intermediate coxae, piceous, sometimes slightly paler at apex of first and second segments.

Antennae: segment I, length .34 mm.; II, 1.2 mm., thickness of apical half (.08 mm.) very little greater than on basal half (.07 mm.); III, .45 mm.; IV, .38 mm.; black, very finely pale pubescent, segment II, with a few hairs equal to thickness of the segment.

Pronotum: length 1 mm., width at base 1.71 mm., anterior angles .88 mm., collar .58 mm.; black, collar except at sides, slenderly on lateral and posterior margins of disk, lower pleural margin to top of coxal cleft, pale to ivory-white; disk moderately convex, closely and rather coarsely punctate, minutely pale pubescent; lateral margins practically straight, perceptibly carinate, anterior angles prominent, posterior angles rounded yet the nearest one-third of basal margin if projected would form a right angle with the lateral margin, the middle one-third slightly sulcate; calli confluent, forming a transverse slightly elevated area, impunctate, shining; propleura closely and coarsely punctate; xyphus distinctly convex, finely pale pubescent. *Scutellum* rather coarsely punctate except nearest the basal margin, black, narrowly at apex and more slenderly at basal angles ivory-white; mesoscutum moderately exposed, black, finely pale pubescent. *Sternum* and pleura black, ostiolar peritreme white.

Hemelytra: width 2.02 mm.; piceous to black, slightly translucent on basal one-fourth of embolium and a small spot near base of corium; glabrous or only minutely and sparsely pubescent, shining, closely and rather coarsely punctate, the heaviest punctures closely placed on the clavus; lateral margin of embolium slightly sinuate, minutely pubescent near the edge. *Cuneus* length slightly greater than width at base, punctate, black, pale and more or less translucent bordering the fracture and inner angle. *Membrane* clear, a distinct fuscous arc in the submargin of the apex, slightly darker at each side; veins fuscous, darker along apex of areoles, the infuscation invading the membrane slightly.

Legs: piceous to black, the femora becoming ferrugino-testaceous toward the apices, not distinctly annulated with paler, rather longly but finely pubescent,

especially on the anterior surface; tibiae triannulate with pale, a narrow basal band just below the knee, frequently nearly obsolete, the broadest band occupying the middle of the apical half; anterior face of tibia armed with a row of brownish spines, in length equal to diameter of the segment, also clothed with numerous rather stiff hairs chiefly shorter than the spines; tarsi blackish, the basal segment paler; claws deeply notched, piceous.

Venter: black, shining, moderately clothed with pale to yellowish pubescence or very fine hairs; genital claspers (Pl. X) distinctive of the species.

♀. Length 4.2 mm., width 2.05 mm.; slightly shorter and more robust than the male but very similar in structure and color; second antennal segment more slender, tapering from base to larger near apex, the middle one-third usually yellowish brown; apex of membrane frequently not so distinctly marked with fuscous.

Holotype: ♀ Aug. 10, Las Vegas, New Mexico (H. S. Barber); Cat. No. 6851, U. S. N. M. *Paratypes*: ♀ Aug. 2, ♀ Aug. 7, ♀ Aug. 8, Las Vegas, N. Mex. (H. S. Barber). Uhler records all four specimens as "secured Aug 10."

Allotype: ♂ Aug. 3, Grand View, Grand Canyon, Arizona (H. H. Knight); Cornell University collection. *Specimens examined* in addition to the types: ARIZONA,—2♂, 8♀ Aug. 2, top Bright Angel Trail, Grand Canyon; 3♂ 3♀ Aug. 3, Grand View, Grand Canyon (H. H. Knight). ♂ July 11, Williams (A. Wetmore). ♂ July 16, Williams (Barber & Schwarz). ♂ 2♀, Prescott. CALIFORNIA,— ♀ April 27, Stanford (Harold Morrison). 3♀ April 12, Oakland (E. C. Van Dyke). ♀ July 14, Mt. Diablo (E. P. Van Duzee). ♂ 2♀, San Berdino (Coquillett). ♀ Jan. 1905, Menlo Park (F. Hornung). COLORADO,—♂ July 18, ♂ 2♀ July 20, Golden (W. J. Gerhard). ♀ April 20, Ft. Collins. ♂ July 9, ♀ July 28, Grand Junction. ♀, Grand Junction (H. Osborn). ♀ July 12, Denver; ♂♀ July 19, Manitou; ♂ July 21, Boulder; ♂♀ July 24, Salida (E. P. Van Duzee). NEW MEXICO,—♂ May 1, 2♀ June 1, Alamogordo. ♀ June 18, Cloudcroft. 2♂ June 2, Highrolls. ♂♀ May to Oct., Fort Wingate. 3♂ 10♀ June 23, Jemez Springs (J. Woodgate). OREGON,—♂ May 28, 1893, Mt. Tabor, Portland. BRITISH COLUMBIA,—♂ April 24, Victoria (A. E. Cameron). ♀ Victoria (G. W. Taylor). ♂ Aug. 9, Royal Oak (W. Downes).

An examination of the types proved this species to be something entirely different from that which the writer, working from the description alone, Reuter, and probably other workers took to be Uhler's *brevis*. The original description is misleading in describing the membrane as "soiled white" when all the type specimens show it to be infuscated in the usual understanding of the term. The species herein de-

scribed as *bakeri* n. sp. is the one that has usually been regarded as *brevis,* for it has a pale or "soiled white" membrane.

Deraeocoris (Camptobrochis) brevis piceatus new variety

Structurally very similar if not identical with *brevis* but differs at least in general color aspect; lateral margins of disk, base of embolium and corium, the clavus largely, pale to yellowish translucent; resembles *nubilus* in coloration but differs in having the central area of pronotal disk black with no indication of a pale median line.

♂. Length 4.8 mm. *Head*: similar to *brevis,* very pale forms may have the juga brownish but never connected with the pale vitta on front.

Pronotum: lateral margins more or less broadly pale, the central area of the disk black, the median line never pale.

Hemelytra: width 2.1 mm.; basal half of embolium and corium and sometimes extending along claval suture, clavus except along claval commissure, and base of cuneus, pale yellowish translucent.

Legs: more broadly pale than in *brevis* and frequently distinctly reddish.

Venter: black, in very pale forms sometimes reddish brown to piceous; genital claspers very similar to if not identical with *brevis.*

♀. Similar to the male in coloration, structurally not differing from *brevis.*

Holotype: ♂ July 24, Golden, Colorado (W. J. Gerhard); author's collection. *Allotype*: topotypic. *Paratypes*: CALIFORNIA, —1♂ 1♀ Aug. 20, Placer Co.; 2♂ Summit, Placer Co. (7,000 ft.); 4♂ 1♀ Aug. 24, Donner Lake, Placer Co.; ♂ ♀ Aug 21, Fallen Leaf, Eldorado Co.; 1♂ 2♀ June 17, Wawona, Mariposa Co. (W. M. Giffard). ♂ 2♀ July 9, Clayton, Shasta Co.; 2♂ 2♀ July 10, Huntington Lake; 2♀ July 23, McCloud, Siskiyou Co.; 3♂ 3♀ July 24, Sisson; 2♀ July 28, Mt. Eddy; 2♂ 1♀ Aug. 2, Hobergs, Lake Co. (E. P. Van Duzee). ♀ Aug. 21, Lake Tahoe (E. L. Diven).) 4♂ 2♀ Placer Co. (Uhler collection). ♂ 4♀ Oct., 1891, Lake Tahoe (Heidemann collection). COLORADO,— ♂ July 28, Grand Junction.   ♂ Grand Junction (H. Osborn).   ♀ July, Cheyenne Canyon, Colorado Springs. 3♂ 4♀ July 24, Salida; ♂ April 27, Fort Collins (E. D. Ball).   ♂ May 11, Graham's Park, Rio delos Pinos, on Salix bloom (C. F. Baker).   IDAHO,— ♀, Couer d'Alene (Uhler collection).   MONTANA,— ♂ 2♀ July 31, Missoula (A. A. Nichol).   ♀ June 30, Bozeman.   ♀ Sept. 6, Bear Paw Mountain.   NEVADA,— ♂♀ "Nev." (Uhler collection).   OREGON, —♀ June 12, Josephine Co. (F. W. Nunenmacher).   2♀, "Oregon" (Koebele).   ♀ June 10, Odell.   10♂♀ Dilley.   WASHINGTON,— ♂, "W. T." (Uhler collection).   ♀ June 30, 1882, Lone Tree, Yakima River.   BRITISH COLUMBIA,—4♀ July 20, Bear Lake; 3♀ Aug. 5, Kaslo (A. N. Caudell).   2♀ July 6, North Bend.   ♀ May 20, Pendleton; ♀ June 4, Royal Oak (R. C. Treherne).

Deraeocoris (Camptobrochis) nubilus new species

Slightly larger than *nebulosus,* most closely related to *brevis* and *validus;* male more elongate than female, apical half of membrane infuscated, usually more so than in *brevis;* general coloration more nearly that of *validus* which species has the membrane merely tinged with fumate.

♂. Length 4.8 mm. *Head*: width .97 mm., vertex .38 mm., length .37 mm.; black, shining, line bordering front margin of eye, carina, juga, median line on front and on tylus, yellowish to ivory-white. *Rostrum,* length 1.75 mm., scarcely attaining the posterior margins of the middle coxae, piceous, slightly paler at the joints.

Antennae: segment I, length .31 mm.; II, 1.22 mm., nearly cylindrical, thickness .085 mm.; III, .40 mm.; IV, .42 mm.; uniformly blackish, pubescence fumate, last three segments beset with several longer infuscated hairs.

Pronotum: length 1.03 mm., width at base 1.7 mm., anterior angles .77 mm., collar .57 mm., nearly as in *brevis;* glabrous, shining, punctures black and prominent; calli confluent, impunctate, black, a pair of deep punctures just behind on the median line; collar pale, extending back from calli usually to basal margin of disk blackish, the lateral areas olivaceo-testaceous to grayish translucent, the median line always more or less pale. *Scutellum* punctate, black and shining, lateral margins basally and the median line apically, ivory-white. *Sternum* and pleura piceous, ostiolar peritreme white.

Hemelytra: width 2.02 mm., longer than in the female, uniformly olivaceo-testaceous or grayish translucent; punctures black, deep and moderately close, extreme outer edge of embolium and the commissure blackish. *Cuneus* punctured and colored as the corium, the apical half dark fuscous to black. *Membrane* infuscated, within the areoles, a transverse area immediately distad of the brachium and cuneus, hyaline.

Legs: posterior femora piceous, yellowish brown to reddish on the apical half and marked with two piceous bands, the extreme apex whitish; middle and front femora with the pale color restricted more to apices, trochanters testaceous; tibiae thrice annulated with fuscous and pale, fuscous band at the apex, middle and just below the knee, a fuscous spot on the knee but pale on the ventral side; tarsi fuscous to blackish, paler near the base.

Venter: black, shining, finely pale yellowish pubescent; genital claspers (Pl. X) distinctive of the species.

♀. Length 4.2 mm., width 2 mm.; shorter and more robust than the male; segment II, length .97 mm., shorter and more slender, nearly as in *brevis,* pale on the middle third; white before the calli and more extensively on the head and scutellum.

Holotype: ♂ Feb. 13, Ithaca, New York (H. H. Knight); author's collection. *Allotype*: same data as the type. *Paratypes*: 8♂ 13♀, taken with the types. CONNECTICUT,—♀ June 13, Rainbow (B. H. Walden), on white pine. DISTRICT OF COLUMBIA,— ♂ July 4, ♂ Nov. 5, Washington (O. Heidemann). MASSACHU-SETTS,—♀ Sept. 14, 2♂ Oct. 8, Forest Hills; ♂ Nov. 1, Northampton (H. M. Parshley). ♂♀ "Mass." (Uhler collection). ♂♀

July 11, Wellesley (E. P. Van Duzee). MINNESOTA,—♀ May 11, Taylor's Falls, on *Pinus strobus* (H. H. Knight). NEW HAMP-SHIRE,—2♀ June 10, Claremont. NEBRASKA,—♀ Aug. 14, Sioux County. NORTH CAROLINA,—♂ July 19, Lake Toxaway (Mrs. A. T. Slosson). NEW YORK,—♀ May 20, ♀ June 14, ♂♀ June 30; ♂ July 8, 4♂ July 13, ♀ July 24, ♂ July 26, on *Pinus strobus;* 2♀ Nov. 6, (in house) Ithaca; ♀ June 22, Portage; ♀ July 14, Batavia (H. H. Knight). 6♂ 6♀ July 11, Taghanic (near Ithaca), taken on *Pinus resinosa* (H. H. Knight). ♀ April 19, (in house) ; ♀ Aug. 16, (at light) White Plains (J. R. Torre-Bueno). VIRGINIA,—♀ Oct. 5, (P. R. Uhler). NOVA SCOTIA,—♀ Sept. 13, Truro (R. Matheson). NEW-FOUNDLAND,—♀ Stephenville, Bay St. George.

The writer found the types and a large series of specimens hibernating under the bark of a log where the insects had collected to spend the winter. When found, some were stiff with frost but soon revived as they were warmed in the sunshine. The writer has taken two specimens late in the fall as they came into buildings evidently seeking hibernation quarters. The species breeds on *Pinus strobus* and *Pinus resinosa* but only in favored spots on certain trees. One specimen was taken on larch, *Larix laricina*, but its occurrence on that tree may be merely accidental. The small white, wax-coated nymphs, were found in company with *Chermes pinicorticis* Fitch, resembling very much the wax-covered aphids. The bug is probably predaceous to a certain extent upon the pine bark aphid altho actual puncturing of an aphid was not observed.

Deraeocoris (Camptobrochis) nubilus obscuripes new variety

Structurally very similar if not identical with *nubilus*, but much darker in color, especially the legs.

♀. Length 4.3 mm., width 2.2 mm. *Head*: black, a small mark on median line of front and the jugae brownish, spot each side of vertex and more broadly along the carina pale.

Antennae: black, structurally not distinguishable from the typical form.

Pronotum: median line of disk reduced to a slender brownish line, lateral margins rather broadly brownish testaceous. *Scutellum* ivory-white at apex and basal angles.

Hemelytra: piceous, base of embolium and corium, central area of clavus, and base of cuneus, brownish testaceous.

Legs: black, hind femora with an obscure reddish black dorsal mark just before and at apex; tibiae with two obscure reddish brown annulations.

Holotype: ♀ June 30, Bozeman, Montana; author's collection.

Deraeocoris (Camptobrochis) nigrifrons new species

Slightly larger than *nebulosus,* very similar to but scarcely as large as *nubilus;* hemelytra of male short, similar to the female; frons black, apical half of membrane infuscated.

♂. Length 3.6 mm.   *Head*: width .94 mm., vertex .43 mm., length .35 mm., black, shining; carina and in paler specimens a spot each side of vertex bordering eye pale; eye slightly smaller and less rounded than in *nubilus,* not occupying as much of the gena as in that species or *nebulosus.* *Rostrum,* length 1.34 mm., nearly attaining the posterior margins of the middle coxae, piceous.

Antennae: segment I, length .30 mm.; II, .91 mm., tapering to slightly thicker from base toward apex, attaining the thickness of segment I, pale yellowish pubescent and beset with several fine erect hairs which in length exceed the thickness of the segment; III, .39 mm.; IV, .37 mm.; black, the last two segments with erect pale hairs as in segment II.

Pronotum: length .91 mm., width at base 1.54 mm., anterior angles .91 mm., collar .67 mm.; nearly as in *nubilus,* the calli more distinctly swollen and confluent, without two deep punctures just behind on the median line; calli and posteriorly black, the median line slenderly pale. *Scutellum* nearly as in *nubilus,* lateral margins and sometimes the median line apically ivory-white. *Sternum* and pleura black, posterior and ventral margins of the epimera pale; ostiolar peritreme white.

Hemelytra: width 1.74 mm., short as in the female; olivaceo-testaceous or grayish translucent, corium except base and spot near tip of clavus, apex of embolium, commissure and more or less along base of clavus piceous, punctures black. *Cuneus* shorter than in *nubilus,* black, the basal half pale translucent, punctures black. *Membrane* infuscated nearly as in *nubilus.*

Legs: black, tips of coxae and margins of trochanters pale, apices of femora pale but with a black saddle-shaped spot over the dorsal half which viewed from above gives the appearance of two annulations; tibiae biannulate and with a third indication ventrally just below the knee, pale; two basal segments of tarsus largely pale.

Venter: black, shining, very finely pale pubescent; genital claspers (Pl. X) distinctive of the species, approaching *brevis* most closely.

♀. Length 1.37 mm., width 2.11 mm., very similar to the male but slightly more robust; very little paler than the male, the median line on pronotal disk usually more broadly pale while the femora are not so distinctly biannulate as in the male.

Holotype: ♂ August 3, Axiel, Colorado; author's collection. *Allotype*: August 24, Donner Lake, Placer County, Cal. (W. M. Giffard); collection of California Academy Sciences.   ♂ ♀, taken with the allotype.

Deraeocoris (Camptobrochis) validus (Reuter)

1909 *Camptobrochis validus* Reuter, Acta Soc. Sci. Fenn., xxxvi, No. 2, p. 58.

Slightly larger than *nubilus,* brownish testaceous, calli black but without blackish rays posteriorly, median line of disk faintly indicated in paler; mem-

brane having only a transverse fumate cloud on the apical half which scarcely attains the margin.

♂. Length 1.6 mm. *Head*: width .94 mm., vertex .4 mm., length .48 mm.; carina present but low and broad, an impression each side on vertex curving forward to the median line, front less convex than in *brevis;* black, carina, along front margin of eyes but interrupted by a spot, juga, tylus except geminate mark on basal half and transversely just before apex, spot below base of antenna and frequently one on the genae, slender lower margin of bucculae, pale. *Rostrum*, length 1.51 mm., reaching upon middle coxae, brownish black, paler at the apex of first and second segments.

Antennae: segment I, length .34 mm.; II, 1.15 mm., nearly cylindrical but slightly more slender on the basal half, pale pubescent, beset with several erect dusky hairs which in length nearly equal thickness of segment; III, .4 mm.; IV, .37 mm.; black, the last two segments with a few fine hairs which are longer than the general pubescence.

Pronotum: length .97 mm., width at base 1.68 mm., anterior angles .84 mm., collar .66 mm.; disk moderately convex, rather coarsely punctate, especially just behind the calli and at each side, lateral margins slenderly carinate and slightly sulcate, the anterior angles distinct and not so broad as in *brevis* or *nubilus;* calli practically flat, separated by two coarse deep punctures, black, just before and somewhat invading the callus at the latero-anterior angle pale; disk brownish testaceous, the median line indicated by slightly paler, devoid of black behind the calli or on the basal angles; propleura brownish, paler on the ventral margin, dorsally either side of the coxal cleft blackish; xyphus pale, disk convex and infuscated, distinctly pale pubescent. *Scutellum* rugose-punctate, dark brownish, the punctures black, apex and the lateral margins basally ivory-white, the median line palely indicated. *Sternum* and pleura black, posterior and ventral margin of the epimera pale brownish; ostiolar peritreme white.

Hemelytra: width 2.05 mm.; scarcely differing from the female, brownish testaceous, rather uniformly black punctate, becoming piceous at apex of corium and a small inconspicuous spot at middle. *Cuneus* pale brownish translucent, punctures and the apex piceous. *Membrane* clear, brachium and slightly invading the membrane dark brownish, apical half with a transverse fumate cloud which scarcely attains the margin.

Legs: more or less pale and with piceous and black; posterior and middle femora broadly biannulate with piceous on the apical half, the basal half with two rows of spots on anterior face, a row of spots or a line on the dorsal surface; front femora black, biannulate with pale brownish near apices; tibiae triannulate with pale, the annulation just below the knee frequently interrupted by a piceous line on the dorsal side; tarsi pale, the apical segment and claws piceous.

Venter: black, shining, very finely pale pubescent; genital claspers (Pl. X) distinctive of the species.

♀. Length 4.8 mm., width 1.96 mm.; very similar to the male, median line of frons pale or brownish; segment II of antennae slender at base and tapering gradually thicker toward apex, not attaining the thickness of segment I, annulated with pale or brownish at middle.

Plesiotypes: ♂ May 3, Milpitas, California (R. J. Smith); ♀, Santa Clara County, California (C. F. Baker); author's collection. *Specimens examined:* CALIFORNIA,—2♀ September, Palo Alto (J. C. Bradley). ♀ Santa Clara County (C. F. Baker) [type material]. ♀ Aug. 2, Lakeport (E. P. Van Duzee). ♀, "Cal." (Uhler collection). OREGON,—♀ May 19, Dalles (U. S. N. M.).

The writer has not seen the type of this species altho type material has been studied. Dr. Philip A. Munz has been kind enough to furnish the writer with a list of the type specimens of Miridae which are found in the Pomona College collection. This list indicates that most of the types are contained there of species described by Reuter from the material collected by Prof. C. F. Baker. Of seven specimens from the type locality one is labeled "Camptobrochis" by Reuter but without specific name written out. This omission was probably due to an oversight which was never corrected following the description of the species.

No data are available regarding the food habits of the species, altho the May and September records indicate that the adults hibernate.

Deraeocoris (Camptobrochis) luridipes new species

Dorsal aspect very similar to that of *validus,* differs in having the apical half of membrane strongly infuscated and in the uniformly lurid or brownish femora.

♂. Length 4.8 mm. *Head:* width .97 mm., vertex .44 mm., length .54 mm.; nearly as in *validus* but the front is perceptibly more convex; carina distinct, indented just before; polished, black, the carina, a longitudinal median spot on front, bordering eyes and projecting slightly on vertex, jugae, spot at middle of tylus, pale yellowish. *Rostrum,* length 1.9 mm., barely attaining posterior margins of middle coxae; black, slightly brownish on under side at base and apex of segments I and II.

Antennae: segment I, length .4 mm.; II, 1.48 mm., gradually thickened from base (.057 mm.) to apex (.085 mm.); pale pubescent, the longest hairs equal to little more than thickness of segment; III, .51 mm.; IV, .40 mm.; black, perceptibly pale at tips of segments I and II.

Pronotum: length 1.14 mm., width at base 1.9 mm., anterior angles .88 mm., gently rounded; collar .65 mm., finely granulate, pale to yellowish; punctuation and surface similar to *validus;* calli black, the pale area just before and bordering the calli stained with brownish; disk uniformly grayish testaceous, devoid of black at the basal angles; propleura testaceous, pale bordering the coxal cavities, dorsally surrounding the coxal cleft and anteriorly to the stricture black; xyphus black, distinctly pale pubescent. *Scutellum* punctate, black, the side margins and apex ivory-white. *Sternum* and pleura black, slenderly brown along the suture separating the meso- and meta-pleural sclerites, pleura distinctly pale pubescent; ostiolar peritreme white.

Hemelytra: width 2.28 mm.; structurally very similar to *validus;* yellowish translucent, punctures black; bordering the commissure, a broad elongate spot occupying the apical half of corium, embolium toward the apex and slenderly along the outer edge, blackish. *Cuneus* testaceous, slightly translucent, punctures and the apical half black. *Membrane* distinctly fuscous on the apical half and projecting basally somewhat between the areoles, veins brownish black at apices of areoles, in darkest specimens somewhat invading the membrane; areoles within, bordering the veins without and at tip of cuneus, pale.

Legs: lurid to translucent brownish, anterior faces of femora with a linear series of fuscous points, the apices narrowly pale; tibiae indistinctly triannulate with paler; tarsi piceous, slightly brownish at base.

Venter: piceous black, shining; genital claspers (Pl. X) distinctive of the species.

♀. Length 4.8 mm.; very similar to the male, head more broadly pale and the corium with very little blackish.

Holotype: ♂ June 21, 1914, San Diego Co., Calif. (E. P. Van Duzee); collection of E. P. Van Duzee.

Allotype: same data as the type. *Paratype*: ♀, taken with the types. Mr. Van Duzee took the specimens on an "elderberry tree."

KEY TO THE SPECIES OF GROUP II

In this group the body form, genital claspers, and punctate scutellum all point to a close relationship with group I, while the non-cleft claws exhibit an affinity with the species of group V. *D. diveni* is very distinct and would merit the separation into a new group were other species discovered having similar characteristics.

1. Dorsum heavily pubescent or hairy   6
   Dorsum glabrous or practically so   2

2. Femora deep black, apices distinctly pale, tibiae biannulate with pale; pronotal disk of female largely pale, the calli and basal angles black; disk of male largely black, narrow median line and a stripe behind lateral angles of calli pale to brownish, black color on frons never forming transverse bars; dorsal width of an eye in the male not equal to width of vertex   .   .   .   .   .   *atriventris* n. sp. p. 112
   Femora not as the above, more or less brownish black or reddish, frequently biannulate with paler on the apical half; tibiae variously banded; dorsal width of an eye in male equal to width of vertex   .   3

3. Femora narrowly pale at apex and a second band just before; hind tibiae distinctly biannulate, a third pale indication just below the knee; hemelytra more or less pale, apex, middle, and narrow base of corium blackish; cuneus black, pale on the basal half   . *incertus* n. sp. p. 114
   Femora pale only at the very apex, or if a second annulation is indicated, then the cuneus reddish; hind tibiae biannulate or banded with pale only on the apical half; cuneus usually reddish, corium sometimes like the above   4

4. Femora uniformly reddish brown, indistinctly pale at the very apex;
    hind tibiae reddish brown, a single pale annulation on the apical half;
    hemelytra, cuneus, and pronotum distinctly tinged with reddish   .
    .   .   .   .   *incertus carneolus* n. var. p. 116
    Femora black, sometimes with more or less pale; hind tibiae blackish,
    biannulate or with only a single pale band on apical half; hemelytra
    and pronotum not tinged with reddish, but pale with fuscous and
    black, cuneus either reddish or black at base   5
5. Hind tibiae black, distinctly annulated with pale on apical half only;
    femora black, slightly pale at tips; cuneus black, pale on basal half,
    frequently tinged with reddish   .   *incertus picipes* n. var. p. 116
    Hind tibiae blackish, biannulate with pale or even with a third pale
    indication below knee; femora brownish black, rather distinctly bian-
    nulate with pale on the apical half; cuneus red or brownish red   .
    .   .   .   .   *rufusculus* n. sp. p. 116
6. Head black, pale color appearing along the median line of front; femora
    and ventral surface piceous, shining, tibiae biannulate with pale; slen-
    der elongate species, dorsum pitchy black and clothed with fine long
    pale hairs   .   .   .   .   *diveni* n. sp. p. 117

Deraeocoris atriventris new species

About the size of *brevis* or *nubilus,* dorsum glabrous, rather coarsely punc-
tate, shining, second antennal segment longer than the head and pronotum
taken together; femora black, only the apices pale, dorsum pallid grayish-
testaceous and marked with black, much darker in the male.

♂. Length 4.7 mm. *Head*: width .98 mm., vertex .38 mm., length .48
mm.; carina delimited behind by a groove, sloping anteriorly to a pair of curved
impressions on vertex, collum broadly exposed, vertex broader than the dorsal
width of an eye; black, carina, spot each side of vertex and curving along
front margin of eye, usually interrupted and leaving a spot just above base
of antenna, and the juga, pale. *Rostrum,* length 1.84 mm., black, attaining the
middle of hind coxae, first segment extending upon basal one-third of xyphus.

Antennae: segment I, length .34 mm.; II, 1.71 mm., nearly cylindrical,
equal to segment I in thickness, pubescence pale and blackish mixed, a few
black exserted hairs which in length are not equal to thickness of segment;
III, .37 mm.; IV, .37 mm.; black, the last two segments slender and beset
with several blackish exserted hairs which in length exceed the thickness
of the segments.

Pronotum: length 1.08 mm., width at base 1.8 mm., anterior angles .74
mm., collar .65 mm.; disk convex, coarsely and rather irregularly punctate, lateral
margins distinct, nearly straight, narrowed in front, the anterior angles little
wider than the collar; calli black, shining, convex and confluent, delimited be-
hind by coarse punctures, disk of each callus with three or four fine punctures
near the latero-posterior angles; disk olivaceo-testaceous, basal angles broadly
black, becoming black along the basal margin and irregularly among the punc-
tures either side of the median line, frequently leaving a paler ray behind
lateral angle of each callus, collar pale; propleura black, ventral and posterior
margins more or less pale; xyphus black, moderately convex, collar pale.

Scutellum punctate, more coarsely and rugose-punctate on the basal half; black, the basal angles and apex ivory-white, mesoscutum black. *Sternum* and pleura black, opaque, the posterior and ventral margins of the epimera sometimes slenderly pale, ostiolar peritreme white.

Hemelytra: width 1.98 mm., brownish testaceous, strongly translucent, punctures black; spot at base, irregularly at middle and the apical area of corium, apex and slender lateral edge of embolium, bordering the commissure, black. *Cuneus* black, more or less pale at base, punctures black. *Membrane* fuscous on apical half, paler within the larger areoles and immediately distad of the brachium, brachium infuscated, the dark color invading the membrane slightly.

Legs: black, shining, tips of coxae and bases of trochanters pale, femora pale only at the apices; tarsi black, claws fusco-translucent, slender and not distinctly cleft; arolia very slender, bristle-like, erect and subparallel, converging slightly at apices (fig. 2, A).

atriventris

Fig. 3. *Deraeocoris atriventris*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: black, shining, pale pubescent; genital claspers (fig. 3) distinctive of the species.

♀. Length 4.8 mm., width 2.2 mm., more robust than the male; dorsum largely pale testaceous, calli and basal angles of pronotal disk black; hemelytra largely pale grayish testaceous, black spot at base and middle, but the blackish color at apex of corium more restricted than in the male; segment II, length 1.57 mm., slender, becoming gradually thicker toward apex, scarcely equaling the thickness of segment I, black, sometimes dark brownish at middle, pale pubescent, a few darker and longer hairs near apex.

Holotype: ♂ July 27, Mt. Lemon (alt. 9,000 ft.), Santa Catalina Mts., Arizona (H. H. Knight); Cornell University collection. *Allotype*: taken with the type. *Paratypes*: 46♂ 42♀ taken with the types.

All the specimens were taken on *Pinus scopulorum* and *P. arizonica* at the top of Mt. Lemon. Nymphs in the fourth and fifth nymphal instars were taken with the adults. A description of the fifth nymphal stage is as follows:

Length 3.3 mm., width (across wing-pads) 1.8 mm. *Head*: width .91 mm., vertex .48 mm., length .63 mm., more flattened and porrect than in the adult; carina not apparent, a row of small black bristles in its stead, triangularly impressed just before on the vertex; several large black bristles on front of head, one at base of jugum and two along lower half of front margin of eye which are most prominent; grayish testaceous, front mottled with fuscous each side of median line, geminate mark on basal half of tylus, along inner margin of eye and above base of antenna, blackish. *Rostrum*, length 1.57 mm., nearly attaining posterior margins of hind coxae, dusky to piceous.

Antennae: segment I, length .25 mm., thickness .09 mm.; II, 1.28 mm., thickness .09 mm., cylindrical, clothed, but not thickly set, with short stiff

black hairs, in length not equaling thickness of segment; last two segments mutilated; fusco-brownish, the basal segment more blackish.

Pronotum: length .65 mm., width at base 1.25 mm., width at anterior angles .83 mm.; disk nearly flat, more convex where the callosities are indicated, grayish testaceous, spotted and marked with fuscous, a row of black bristles on the anterior submargin; lateral margins nearly straight, beset with several bristles, basal margin sulcate at middle and broadly curving to the basal angles; propleura much reduced, coxal cleft distinct and cut well up under the lateral margin of disk, xyphus poorly developed. *Mesonotum* smooth, median line apparent as a fine impression which continues forward upon the pronotum; wing-pads reaching to posterior margin of the fourth visible abdominal segment, ground color similar to pronotum but more closely spotted with fuscous, the apical area, base, and the mesonotum largely clouded with fuscous; lateral margins of wing-pads beset with short stiff black bristles.

Legs: black, apices of femora pale; hind tibiae biannulate with pale, a third annulus indicated beneath the knee; front and middle tibiae more broadly pale, the three fuscous annulations much reduced, black on the knee; tibial comb fully developed and similar to that of the adult; tarsi two-segmented, the second segment three times the length of the first, blackish; claws as in the adult, arolia not distinguishable.

Abdomen: testaceous, ten segments visible from the dorsal aspect, a sparsely set row of black bristles transversely across the middle of each segment, each bristle usually arising from a fuscous spot; the third tergite and half of the fourth covered at middle by a conspicuous opaque blackish spot; tergites 5-8 with a dark opaque spot at each side in the lateral submargin, placed nearest the anterior margin of the tergite, the largest spot on the eighth tergite; spiracles situated on the ventral submargin and corresponding closely in position with the dorsal spots just described. The anus is provided with an eversible organ of sticky nature which enables the nymph, when disturbed and falling from one limb to another, to attach itself to the first object it strikes until such time as the feet can be brought into use again.

Deraeocoris incertus new species

Slightly larger than *atriventris,* femora biannulate with pale on the apical half; base, middle, and apex of corium piceous; eyes of male large, width of vertex not equal to the dorsal width of an eye; segment II of male antennae with fine short pubescence, devoid of exserted hairs.

♂. Length 5 mm. *Head*: width 1.06 mm., vertex .35 mm., length .54 mm.; carina much flattened, produced forward at the median line, a groove separating it from the collum; collum broadly exposed, black; eyes large, dark brown, nearly ovate when viewed from the side, much reducing the genal area; black, the pale markings very similar to those of *nubilus,* carina, bordering front margin of eye below vertex, median line of front below vertex and connecting beneath with juga, small spot below base of antenna, the median and a lateral line on tylus, pale or white. *Rostrum,* length 1.85 mm., reaching upon the hind coxae, piceous.

Antennae: segment I, length .34 mm., brownish black, paler on the apical half; II, 1.65 mm., cylindrical, equal in thickness to segment I, constricted at

base, black, finely pale pubescent; III, .43 mm.; IV, .43 mm.; last two segments slender, black, pale pubescent.

Pronotum: length 1.11 mm., width at base 1.82 mm., anterior angles .83 mm.; collar .68 mm., pale, opaque; disk moderately convex, glabrous, shining, rather coarsely punctate and especially so just behind the calli; lateral margins nearly straight, slenderly carinate, anterior angles narrowed, little wider than the collar; calli moderately convex, smooth and shining, confluent, delimited behind by an impression and also by coarse punctures; calli black but pale just before, median line but more broadly just behind calli, a rather broad ray behind lateral angle of each callus, and slender basal margin of disk, pale; propleura punctate, blackish, more or less pale around the margins; xyphus convex, blackish, the carinate lateral margins and in front on collar pale. *Scutellum* punctate, moderately convex, basal angles, apex, and usually the median line pale or ivory-white; mesoscutum black, distinctly exposed. *Sternum* black, opaque, only a spot at the dorsal margin of the episterna shining; ostiolar peritreme white, posterior and ventral margins of the epimera pale.

Hemelytra: width 2.14 mm., costal margin nearly straight or only very slightly arcuate; corium and clavus slightly more convex than in *atriventris*, coarsely punctate, more closely near the claval suture, glabrous, shining; pallido-testaceous, rather broadly across apex of corium and embolium, narrowly at base, a transverse blotch at middle of corium which continues along claval suture and across apex of clavus, piceous; punctures, slender edge of embolium and inner margins of clavus blackish. *Cuneus* pale, usually the apical half and the punctures blackish. *Membrane* pale fuliginous, apical half, the brachium and somewhat invading the membrane, infuscated, a clear spot bordering apex of cuneus.

Legs: apices of coxae and bases of trochanters pale, femora reddish brown or blackish, biannulate with pale at apices, front pair more distinctly so; hind femora usually more or less pale at middle on the anterior face; tibiae biannulate with pale, the hind pair with a third pale indication just below the knee, a row of spines on the anterior face; tarsi blackish, claws slender, not toothed at base, fusco-translucent; arolia simulating fine bristles, translucent, inclined forward between the claws, nearly parallel but converging slightly at tips.

Fig. 4. *Deraeocoris incertus*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: black, shining, rather sparsely pale pubescent; genital claspers (fig. 4) distinctive of the species.

♀. Length 4.9 mm., width 2.37 mm.; very similar to the male but more robust, usually more broadly pale. *Head*: width 1.05 mm., vertex .44 mm., the dorsal width of an eye not equal to the width of vertex; median line of frons usually joined with the pale on vertex and carina, the black each side of frontal line frequently broken by transverse pale bars. *Antennae*: segment II, length 1.51 mm., slender and brownish on the basal half, distinctly thickened toward apex, a few exserted hairs equal to thickness of segment.

Holotype: ♂ August 12, Portland, Oregon (A. A. Nichol); author's collection. *Allotype*: taken with type. *Paratypes*: 3♀, topo-

typic. CALIFORNIA,—2♀ Aug. 24, Summit (alt. 7,000 ft.), Placer County (W. M. Giffard). ♀ July 28, Mt. Eddy (E. P. Van Duzee). BRITISH COLUMBIA,—♀ July, 1914, Vancouver (R. H. Crystal).

Deraeocoris incertus picipes new variety

♀. Length 5.5 mm., width 2.71 mm., larger than the typical *incertus,* vertex more distinctly indented but otherwise does not appear to differ structurally; femora uniformly piceous, slightly pale only at the very apex; hind tibiae black, distinctly annulated with pale only on the apical half; apical half of hemelytra more broadly piceous than the typical form, cuneus black, pale on basal half, frequently tinged with reddish.

Holotype: ♀ July 26, Webber's Camp (alt. 7,800 ft.), Santa Catalina Mts., Arizona (H. H. Knight); Cornell University collection. *Paratype*: ♀ Aug. 4, Williams, Arizona (H. H. Knight).

Both specimens were beaten from white oak *(Quercus sp.?)* but owing to the isolated specimens taken the occurrence on that tree may have been merely accidental. This form may prove to be distinct from *incertus* but in the absence of male specimens the identity can not be established with certainty.

Deraeocoris incertus carneolus new variety

♀. Length 4.7 mm., width 2.28 mm., nearly the size of the typical *incertus,* marked similarly to *picipes* but all the black color replaced by reddish brown and becoming piceous only in the darkest spots; vertex distinctly indented just before the carina; femora uniformly reddish brown, indistinctly pale at the very apex; hind tibiae reddish brown, a single pale annulation on the apical half; hemelytra, cuneus, and pronotum distinctly tinged with reddish, becoming brownish in the darker parts.

Holotype: ♀ August 2, Huachuca Mts., Arizona (H. G. Barber); author's collection.

Deraeocoris rufusculus new species

Closely related to *incertus,* smaller, darker colored, the cuneus red; segment II of antennae beset at intervals with erect hairs which in length equal the thickness of the segment; the genital claspers indicate a close relationship with *incertus* but certain differences are apparent (fig. 5).

♂. Length 4.9 mm. *Head*: width 1 mm., vertex .29 mm., length .57 mm.; vertex not equal to the dorsal width of an eye, carina low but apparent, arcuated cephalad, an oblique impression each side of vertex which unite on median line at base of frons; collum broadly exposed, a groove separating it from the carina; color markings nearly identical with *incertus. Rostrum,* length 1.98 mm., nearly attaining posterior margins of hind coxae, piceous.

Antennae: segment I, length .34 mm., fusco-brownish and somewhat translucent; II, 1.56 mm., brownish black, cylindrical, perceptibly thicker than segment I, constricted at base, clothed with fine dusky pubescence, beset at intervals with erect hairs which in length equal the thickness of the segment; III, .41 mm., slender, blackish, beset with erect hairs which in length exceed thickness of segment; IV, missing.

Pronotum: length 1 mm., width at base 1.68 mm., anterior angles .77 mm., collar .63 mm.; very similar to *incertus* except that the disk is more coarsely punctate behind the calli; dark brownish to black, shining, slender median line and the basal margin of disk pale or white, just before calli and an irregular spot behind the outer angles pale. *Scutellum* punctate, rather coarsely rugose-punctate on the basal half; dark brownish black, basal angles and apex ivory-white, median line palely indicated near apex. *Sternum* more brownish at the sides than in *incertus*.

Hemelytra: width 1.98 mm., similar to *incertus* except for the color; dark fusco-brownish, translucent, somewhat paler each side of the scutellum. *Cuneus* dark red, slender margin bordering the membrane dark brownish. *Membrane* marked similarly to *incertus* but the infuscation darker, invading the membrane more extensively each side of the brachium.

rufusculus

Fig. 5. *Deraeocoris rufusculus*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Legs: marked similarly to *incertus* but the dark color more brownish than black.

Venter: dark brownish to piceous, shining, rather sparsely pale pubescent; genital claspers (fig. 5) distinctive of the species.

Holotype: ♂ August 12, Portland, Oregon (A. A. Nichol); author's collection.

Deraeocoris diveni new species

Larger than *incertus*, and more elongate, black, shining, pale pilose above; median line of front and tylus and the tip of the scutellum more or less pale, tibiae biannulate with pale.

♂. Length 6.4 mm. *Head*: width 1.03 mm., vertex .45 mm., length .51 mm.; carina absent, vertex abruptly declivous behind, collum narrowly exposed; black, shining, tylus and juga distinctly pale pilose; median line of frons and spreading to form a triangle on vertex, more distinctly on median line of tylus, lower margins of bucculae and extreme tip of tylus, pale or white. *Rostrum*, length 1.85 mm., reaching upon the middle coxae, black, paler at apex of first and second segments.

Antennae: segment I, length .43 mm., strongly narrowed basally, longly pale pubescent on the apical half; II, 1.42 mm., thickness .10 mm., slightly thicker than segment I, nearly cylindrical but narrowed at base and slightly so at apex, black, the extreme tip white, pale pubescent, several exserted hairs slightly darker and in length exceeding the thickness of the segment; III, .52 mm.; IV, .45 mm.; black, the last two segments slender, beset with exserted hairs which in length are nearly equal to twice the thickness of the segment.

Pronotum: length 1.28 mm., width at base 2.05 mm., anterior angles .83 mm., collar .68 mm.; black, opaque; disk punctate, more deeply and coarsely behind the calli and laterally, longly pale pilose, more heavily at the sides, lateral margins distinct, nearly straight, distinctly narrowed at anterior angles, little wider than the collar; calli slightly convex, confluent, disk of each beset with four or five pilose hairs, a pair of large deep punctures just behind, one set each side of the median line; black, shining, basal margin narrowly pale; propleura black, coarsely punctate, pale bordering the coxal cavity, opaque each side of the coxal cleft; xyphus nearly flat, lateral margins much produced or carinate bordering the coxal cavity, black, opaque, pale in front on collar. *Scutellum* black, convex, apex sharply depressed and white; rather indistinctly rugose-punctate (badly injured by the pin, which prevents accurate judgment of the punctate character). *Sternum* and pleura black, granulate and somewhat wrinkled; ostiolar peritreme white.

Hemelytra: width 2.51 mm.; elongate, black, somewhat translucent, rather coarsely punctate; palely pilose, more thickly on embolium and base of corium. *Cuneus* black, pubescent, punctures distinct, pale spot at outer basal angle. *Membrane* infuscated, the brachium and within the areoles slightly darker, a clear spot bordering the tip of cuneus.

Legs: black, tips of coxae and bases of trochanters pale; femora rather slender, tibiae biannulate with pale, devoid of spines except at apices but beset with several prominent hairs; tarsi black, slightly paler on the two basal segments which are practically subequal in length; claws slender, translucent, not toothed at base, arolia simulating fine bristles, pale translucent, inclined forward away from tarsus, nearly parallel but converging at tips.
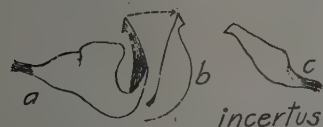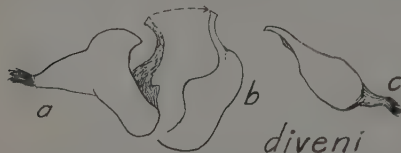

diveni

Fig. 6. *Deraeocoris diveni,* male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: black, shining, rather sparsely pale pubescent; genital claspers (fig. 6) distinctive of the species.

Holotype: ♂ August 26, 1915, Canon Camp (alt. 7,700 ft.), Yellowstone Park, Wyoming (E. L. Diven); author's collection.

This species is named in honor of the young and enthusiastic collector, Mr. Emerson L. Diven who lost his life August 7, 1919, in an airplane accident while scouting in the interest of the pink bollworm control in Texas.

Only the single specimen has been seen by the writer but it is very likely that more material can be obtained by beating conifers at the type locality or at similar altitudes in that general region.

KEY TO THE SPECIES OF GROUP III

1. Tibiae banded with fuscous or pale   2
   Tibiae uniformly pale or yellowish   9
2. Membrane with a distinctly rounded fuscous spot on the apical half,
   frequently connected at base by a fuscous streak extending down from

between the areoles, thus leaving a large pale spot each side of middle
and bordering apex of cuneus 3
Membrane usually somewhat infuscated but not as described above . 4

3. Calli solid black, a broad piceous ray behind each; in pale specimens
the calli may be somewhat brownish but in such case the median line
and margins of the disk are distinctly pale, leaving a dark brown ray
behind each callus; hemelytra with piceous on clavus and corium, em-
bolium pale . . . . . . *borealis* Van D. p. 120
Calli more or less invaded with brownish or pale, distinct rays not ap-
parent behind calli; hemelytra and pronotum more uniformly colored,
either fulvo-testaceous or dark brownish . . . . . .
. . . . *fasciolus* n. sp. p. 123

4. Rostrum extending slightly beyond the posterior margins of the hind
coxae; membrane with the apical half scarcely infuscated, femora pale
but with two distinct blackish bands near apices, hind tibiae biannu-
late with fuscous on the basal half . . *grandis* Uhler p. 126
Rostrum scarcely attaining the posterior margins of the hind coxae;
membrane, femora, and hind tibiae not having the above combination
of characters 5

5. Femora uniformly dark on the apical half, likewise the basal part in
darkest specimens; venter distinctly reddish, sometimes dark chest-
nut red, shining . . . . . . *betulae* n. sp. p. 129
Femora with the apical half distinctly banded or entirely pale . . 6

6. Second antennal segment with prominent pale exserted hairs, in length
equal to three times the thickness of the segment; pronotum with dis-
coidal margins pale, calli and posteriorly on disk black, frequently
forming a ray behind each callus and thus leaving the median line pale 7
Second antennal segment without prominent exserted hairs, or if pres-
ent, not equal to more than twice the thickness of the segment; pro-
notal disk without distinct rays, or if black then the lateral margins
not distinctly paler 8

7. Median line of pronotal disk pale, the black color forming a distinct
ray behind each callus; impressed spot each side of vertex next to eye,
pale, frequently black just beneath the impressed spot and on front
. . . . *alnicola* n. sp. p. 132
Median line of pronotal disk not distinctly pale, sometimes the central
area of disk may be paler than immediately behind the calli but a dis-
tinct median line is not formed; black spot, slightly impressed, one each
side of vertex next to eye, the front more or less black, the median
line usually pale . . . . . . *shastan* n. sp. p. 133

8. Pronotum, sternum, and venter uniformly dark brownish black, a paler
spot at the median line just in front of calli; disk of pronotum slen-
derly margined with pale; hemelytra brownish black, paler parts
stained with brownish . . . . *triannulipes* n. sp. p. 137
Pronotum, sternum, and venter paler, usually pallid gray with fuscous,
in darkest specimens blackish but the median line on pronotum and
scutellum pale; hemelytra with infuscation appearing first at tip of
embolium, on middle, outer margin at apex, and at base of corium,
paler parts more or less translucent; darkest specimens becoming

blackish but the paler and translucent part not stained with brownish
.   .   .   .   *aphidiphagus* n. sp. p. 134

9. (1) Hind femora with two brown or fuscous bands near apices;
apical half of the membrane with a distinctly rounded fuscous spot,
usually connected at base by a fuscous streak which extends up be-
tween the large areoles   10
Hind femora with but one fuscous band; apical half of membrane pale
or clouded with fuscous but the fuscous area not forming a rounded
spot on the apical half   11

10. Calli solid black, a broad piceous ray behind each; in pale specimens
the calli may be somewhat brownish but in such cases the median line
and margins of disk are distinctly pale, leaving a dark brown ray be-
hind each callus; hemelytra with piceous on clavus and corium, em-
bolium pale   .   .   .   . *borealis* Van D. p. 120
Calli more or less invaded with brownish or pale, distinct rays not ap-
parent behind calli; hemelytra and pronotum more uniformly colored,
fulvo-testaceous to dark brownish   .   *fasciolus castus* n. var. p. 125

11. Dorsum uniformly brownish black, or pronotum rich fulvous brown and
the calli not margined or lined with black but uniformly colored as the
disk of pronotum   14
Dorsum pale to testaceous and brownish, frequently becoming fuscous
or blackish but always with some pale; calli margined with black or
entirely black   12

12. Calli black only around the margin, dorsum rich brownish to fusco-
brownish, shining   .   .   *nitenatus* n. n. (=|| *nitens* Reut.) p. 141
Calli entirely black, or if not, then the dorsum pallid testaceous and
with three irregular fuscous spots, one at apex, middle, and base of
each hemelytron   .   .   .   . `.   .   . 13

13. Dorsum fuscous to blackish, usually with a pale median line running
over the disk and scutellum, hemelytra darkened to such an extent that
three fuscous spots are not apparent   .   .   *quercicola* n. sp. p. 138
Dorsum pallid testaceous and with three irregular fuscous spots, one at
base, middle, and apex of each hemelytron; calli usually black but in
pale specimens only margined with black   .   .   .   .
.   .   .   .   *quercicola pallens* n. var. p. 140

14. Dorsum uniformly brownish black; calli and scutellum blackish similar
to the whole dorsum   .   .   .   .   *davisi* n. sp. p. 140
Dorsum largely rich fulvous brown; calli not margined with black but
uniformly colored as the disk of the pronotum; males becoming black-
ish on the basal half of the disk and on the anterior margin, while in
darkest specimens even the calli may become dark but the scutellum
always remains fulvous   .   .   :   .   .   .   .   *fulvus* n. sp. p. 144

Deraeocoris borealis (Van Duzee)

1920 *Camptobrochys borealis* Van Duzee, Proc. Cal. Acad. Sci., ser. 4, ix, p. 354.

Length 6-7 mm. Elongate, largely pale and marked with piceous; calli
deep black, a broad piceous ray behind each, thus leaving the median line and
margins of the disk pale or testaceous; embolium pale translucent, membrane

with a distinctly rounded fuscous spot on the apical half, usually connected at base by a fuscous streak extending down from between the areoles.

♂. Length 6.8 mm. *Head*: width 1.11 mm., vertex .52 mm., length .65 mm.; eyes ovate when viewed from the side, sloping, the lower margin somewhat removed from base of head; front broad, moderately convex, smooth and shining, lower part of face pubescent; carina flat, delimited behind by a groove which separates the black and broadly exposed collum from the vertex; median line of front pale, dark brownish to black at each side, frequently broken into transverse bars; base of tylus and a geminate mark on the basal half, above base of antenna, dorsal margins of lorae and bucculae, spot beneath eye, and narrow tip of tylus, blackish. *Rostrum*, length 2.28 mm., reaching to near posterior margins of the middle coxae, brownish, the apex becoming piceous.

Antennae: segment I, length .57 mm., scarcely reaching beyond tip of tylus by half its length, black, sometimes brownish black; II, 1.71 mm., nearly cylindrical, more slender at base, not equaling the thickness of segment I, rather thickly and longly pale pubescent, length of many hairs equal to twice the thickness of the segment, black, frequently brownish black at base; III, .74 mm.; IV, .56 mm.; last two segments slender, brownish to black, pale pubescent, many of the fine hairs equal to more than twice the thickness of the segment.

Pronotum: length 1.48 mm.; width at base 2.42 mm., anterior angles 1 mm.; collar .8 mm., opaque or dull brownish; disk moderately convex, black punctate, more coarsely just behind the calli, lateral margins distinct, slenderly carinate, nearly straight, narrowed until the anterior angles are little wider than the collar; calli moderately convex, smooth and shining, delimited posteriorly by an impression and coarse punctures, partially confluent but separated by a pair of deep punctures; calli deep black, also an arc projecting forward at the anterior angles, a broad piceous ray behind each callus extending to near the basal margin of disk, the median line broadly, lateral and basal margins of disk and just before the calli, pale to testaceous; propleura punctate, brownish, surrounding the dorsal half of the coxal cleft black and opaque; xyphus slightly convex anteriorly, pale yellowish brown, margins prominently carinate bordering the coxal cavity. *Scutellum* impunctate, convex, shining, pale to testaceous, a piceous vitta each side of median line at base, the piceous color frequently replaced by dark brown. *Sternum* black or brownish black, opaque, a small spot dorsally on the meso- and meta-episterna shining, basalar plate yellowish brown; ostiolar peritreme largely pale but becoming infuscated dorsally.

Hemelytra: width 2.85 mm.; moderately convex, margin of the embolium sinuate arcuate, cuneus and membrane moderately deflexed; glabrous, shining, black punctate; pale brownish translucent to dark brownish and piceous, embolium and narrowly at base of corium pale translucent, clavus dark brownish, more piceous on the basal half and at commissure, corium more or less piceous either side of the cubitus on the apical half. *Cuneus* pale translucent, punctures not evident except at base, apex blackish on the margin bordering the membrane. *Membrane* with a distinctly rounded fuscous spot on the apical half, usually connected at base by a fuscous streak extending down from between the areoles, thus leaving a large pale spot each side of middle and next to apex of cuneus; brachium infuscated, the infuscation invading the membrane each side, larger areole rather elongate and not broadly rounded apically.

Legs: pale testaceous, anterior face of coxae with prominent pale pubescence, ventral margin of femora beset with long pale pilose hairs; femora becoming darker near tips, usually banded twice on the apical half with blackish, in darkest specimens the hind pair frequently broadly black and the bands confluent; tibiae beset with stiff hairs but not with true spines except at tips, in dark specimens the hind pair may sometimes be annulated with fuscous on the basal half; tarsi infuscated at tips, first and second segments subequal in length; claws brownish translucent, deeply cleft or toothed at base, arolia simulating fine bristles, pale translucent, inclined forward, nearly parallel but converging slightly at apices.

borealis VanD.

Fig. 7. *Deraeocoris borealis,* male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: dark brownish to piceous, shining, longly pale pubescent; genital claspers (fig. 7) distinctive of the species, the left clasper without a projecting horn at base.

♀. Length 6.4 mm., width 3 mm.; general coloration very similar to the male, the rays on pronotum sometimes more dark brown than piceous but rays are always apparent, in pale specimens the median line is always paler than at either side behind the calli; scutellum frequently dark brown each side of the median line rather than piceous, the black color on head and sternum much reduced also; segment II of the antennae slender, becoming thicker only on the apical one-fourth, black, sometimes brownish on the basal half, longly pubescent or hairy, length of exserted hairs equal to three times the thickness of the segment.

Plesiotypes: ♂♀ [*paratypes*] July 27, McLean, New York (H. H. Knight); author's collection. *Specimens examined*: *Paratypes*: 1♂ 1♀ July 9, Portland, Maine (E. P. Van Duzee). ♂ June 16, ♀ June 24, ♂♀ June 25, ♂ July 4, ♂ July 18, Batavia; 2♀ July 26, Ithaca; 2♀ June 27, Portageville; 3♀ July 27, McLean Bogs, Tompkins County, New York (H. H. Knight). *Records*: CONNECTICUT,—♀ July 6, South Meriden (H. Johnson). MAINE,—♂ June 26, ♂ July 31, Peaks Island (G. A. Moore). MASSACHUSETTS,—♂ Aug. 8, Chester (C. W. Johnson). MICHIGAN,—2♂ July 5, ♀ July 14, ♀ July 25, Cheboygan County (E. P. Butler). NEW JERSEY,—♂ 3♀ June 18, Hewitt (Wm. T. Davis). NEW YORK,—♀ July 8, Ithaca; 4♂ 2♀ July 3, McLean Bogs, Tompkins County (H. H. Knight). 5♂ 8♀ June 21, Olivera; 1♂ 1♀ July 4, Plattsburg (Wm. T. Davis). ♂ July 15, Wanakena; ♂♀ July 17, ♀ July 20, ♂ July 29, Cranberry Lake (C. J. Drake). ♂ June 24, Rockaway Beach, Long Island (C. E. Olsen). 3♂ July, Olivera (E. Shoemaker). OHIO,—♀ June

29, Delaware (C. J. Drake). WISCONSIN,—3♀ Aug. 12, Salmo, Bayfield County (W. L. McAtee). ONTARIO, CANADA,—3♂ July 3, Lake of Bays (J. McDunnough). NOVA SCOTIA,—♂, Halifax (E. P. Van Duzee).

The writer has taken this species on alders, a few specimens being collected on other plants but always in damp, cool, shaded situations. At the McLean bogs specimens were swept from aphid-curled leaves but the aphid was not identified. *Borealis* is doubtless predaceous to a large extent as is true of *alnicola,* the latter species apparently being confined to alders in its breeding habits. Both species are very similar in general coloration but structurally are very distinct.

Deraeocoris fasciolus new species

Slightly smaller than *borealis,* disk of pronotum more uniformly colored, distinct rays not apparent behind the calli; left genital clasper very similar to that of *borealis* but the right clasper is distinctive.

♂. Length 6.4 mm. *Head*: width 1.06 mm., vertex .51 mm., length .63 mm., structurally not differing appreciably from *borealis;* yellowish brown, spot each side of vertex, four or five transverse spots each side of median line of front, above and below base of antenna, base and apex and two longitudinal stripes on tylus, bucculae, tip of lorae and more or less on juga, blackish. *Rostrum,* 2.17 mm., reaching to near posterior margins of the middle coxae, yellowish to brownish, piceous at apex, the basal segment somewhat infuscated.

Antennae: segment I, length .54 mm., black; II, 1.57 mm., black, somewhat brownish at middle, pale pubescent, longest hairs scarcely equaling twice the thickness of the segment; III, .7 mm., blackish, paler at base; IV, .48 mm., blackish.

Pronotum: length 1.4 mm., width at base 2.28 mm., anterior angles .94 mm., collar .74 mm.; structurally very similar to *borealis,* disk more closely but irregularly punctate; calli dark brownish to black, invaded by pale or brownish at the latero-anterior angles; disk rather uniformly dark brownish, sometimes slightly paler on the central area but never forming distinct rays behind the calli, the lateral margins not at all paler than behind the calli. *Scutellum* impunctate, convex and shining, brownish, the basal angles and apex pale, median line brown, brownish black at each side but not attaining the base, the blackish color never beginning at base as is the case in *borealis.* *Sternum* brownish to black, always paler at the median line, basalar plate yellowish; ostiolar peritreme largely pale but becoming infuscated dorsally.

Hemelytra: width 2.77 mm., structurally very similar to *borealis;* rather uniformly dark brownish to piceous, paler on basal half of embolium and along base of cubitus. *Cuneus* pale translucent, fine infuscated punctures evident, apex more broadly infuscated than in *borealis*. *Membrane* nearly as in *borealis,* the rounded spot on apical half joined at base by a ray-like infuscation produced from the apical angle of each large areole, or in paler specimens not connected but the base of the apical spot not so clearly rounded as in *borealis.*

Legs: structurally as in *borealis;* pale to yellowish, femora biannulate with

blackish on the apical half, the front and middle pair paler on the ventral sur-
face or the bands even obsolete above; tibiae with spot on knee and two annu-
lations on basal half blackish, frequently the apices also darkened; tarsi dark
brownish to blackish, darker at apices.

Venter: dark brownish
to piceous, shining; gen-
ital claspers (fig. 8) dis-
tinctive of the species,
the left clasper differing
very slightly from that
of *borealis*, but the much
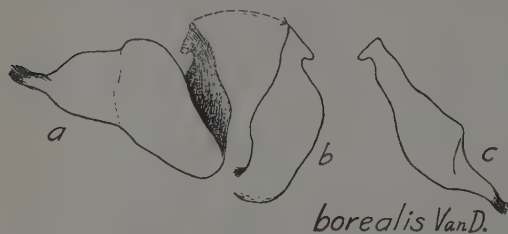more bent and different-
ly shaped right clasper is
distinctive.
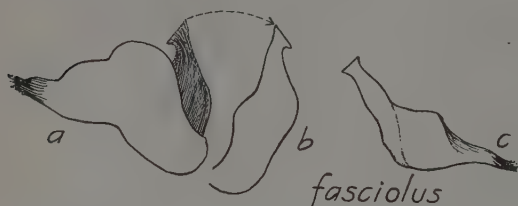
Fig. 8. *Deraeocoris fasciolus*, male genital claspers.
a, left clasper, lateral aspect; b, internal arm of left
clasper; c, right clasper, lateral aspect.

♀. Length 6.5 mm.,
width 3.1 mm.; very similar to the male in coloration but usually not so dark;
segment II, length 1.63 mm., slender and only slightly thicker at apex, black,
testaceous near middle but more broadly black at base than apex, clothed with
fine pale hairs, length of several equal to more than twice the thickness of
segment; paler specimens may have the front of head and calli more broadly
brownish.

Holotype: ♂ July 8, Ithaca, New York (H. H. Knight); author's
collection. *Allotype*: same data as the type. *Paratypes*: NEW YORK,
—2♀ July 8, ♂ 2♀ July 26, ♀ July 23, Ithaca; ♂ June 30, 2♂ July 5,
♀ Aug. 10, ♂ Aug. 13, Batavia (H. H. Knight). ♀ June, ♂ July 2,
Ithaca (W. H. Wellhouse), reared on Crataegus. ♂ July 26, Cran-
berry Lake; ♂ Aug. 1-7, Wanakena (C. J. Drake). ILLINOIS,—♀
June 29, Willow Springs (W. J. Gerhard). MAINE,—♂ July 12,
♀ July 28, Orono (C. W. Johnson). ♀, "Me." (Uhler collection).
MASSACHUSETTS,—♂ Aug. 8, Chester (C. W. Johnson). MICH-
IGAN,—♂ July 11, North Muskegon (C. A. Hill). ♂ Aug. 28,
Marquette. MINNESOTA,—♀ July 20, Gray Cloud Island; ♀ Aug.
18, Elkhorn Creek, Carlton Co.; 3♀ Aug. 30, Two Harbors; ♀ Aug. 20,
Beaver Bay (H. H. Knight). 1♂ 1♀ July 11, Becker Co. (A. A.
Nichol). OREGON,—2♀ Aug. 12, 2♀ Aug. 17, Portland (A. A.
Nichol). WISCONSIN,—3♀ Aug. 12, Salmo, Bayfield Co. (W. L.
McAtee). CANADA: BRITISH COLUMBIA,—3♂ 1♀ July 13,
Kaslo (A. N. Caudell). NOVA SCOTIA,—♀ Aug. 12, Truro (R.
Matheson). ♀ July 26, ♂ July 28, ♀ Aug. 11, ♂ Aug. 19, Smith's Cove
(W. H. Brittain). ONTARIO,—♂ July 14, New Castle (L. Caesar),
"on pear and apple." 3♂ 3♀ Aug. 6, Parry Sound (H. S. Parish).
QUEBEC,—2♂ 1♀ July 22, Lacolle (G. A. Moore).

At Batavia the writer found this species on apple trees always
closely associated with the rosy aphid, *Aphis sorbi* Kaltenbach. The

white wax-coated nymphs frequent the aphid-curled leaves, feeding on the aphids and honeydew excretions. The bugs were never observed to feed on the fruit and it seems to the writer that the species is likely to prove beneficial rather than injurious. The species was also taken on Crataegus, where it was found associated with and predaceous upon *Schizoneura crataegi* Oestlund. Dr. W. H. Wellhouse reared a specimen from the time of hatching to the adult stage on the foliage of Crataegus, altho in rearing other specimens he found that aphids were fed upon when available. The young nymphs appeared with the unfolding of the buds, doubtless hatching from eggs which passed the winter in the buds or twigs. Prof. L. Caesar found *fasciolus* rather abundant on apple and pear trees in Ontario but as yet has not observed it feeding on the fruit.

For a considerable period the writer had considered this species as merely a variety of *borealis* but a close examination of the genital claspers revealed the fact that *fasciolus* is structurally distinct, a point first suggested after observing the habits of these insects.

Deraeocoris fasciolus castus new variety

Apparently only a color form of *fasciolus* but at least a well defined and stable color variety; dorsum fulvo-testaceous, calli usually lined with black but sometimes entirely brownish.

♂. Length 6 mm. *Head*: width 1.08 mm., vertex .51 mm., length .57 mm.; fulvo-testaceous or brownish, basal spot and geminate mark on basal half of tylus, spot beneath eye, dorsal margin of lorae, mark on bucculae and tip of tylus, blackish. *Rostrum*, length 2.28 mm., nearly attaining the posterior margins of middle coxae, yellowish brown, the apex darker.

Antennae: segment I, length .57 mm., yellowish, becoming infuscated on basal half; II, 1.71 mm., pale yellowish, becoming infuscated at apex; III, .68 mm.; IV, .46 mm.; last two segments yellowish or becoming dusky.

Pronotum: length 1.45 mm., width at base 2.39 mm., anterior angles .92 mm., collar .74 mm.; uniformly fulvo-testaceous or brownish, calli lined with black, sometimes entirely brownish. *Scutellum* fulvo-testaceous, basal angles narrowly and sometimes the apex pale. *Sternum* uniformly brownish; ostiolar peritreme pale yellowish, fusco-brownish dorsally.

Hemelytra: width 2.85 mm.; uniformly fulvo-testaceous or brownish, embolium pale translucent, punctures black. *Cuneus* pale translucent, punctures not evident, fusco-brownish on the inner margin at apex. *Membrane* with a rounded fusco-brownish spot on apical half, sometimes produced basally in a ray between the larger areoles, brachium and invading the membrane either side fusco-brownish, in darker forms the areoles also clouded.

Legs: pale yellowish to brownish, sometimes the hind femora with two fuscous bands near apices; tibiae pale or with only a spot at knee; tarsi darkened at apices, claws brownish translucent.

Venter: testaceous to rich dark brownish, shining; genital claspers very similar if not identical with those of *fasciolus*.

♀. Length 6.5 mm., width 3 mm.; similar to the male in coloration; segment II, length 1.71 mm., pale yellowish, the apex infuscated.

Holotype: ♂ July 23, Ithaca, New York (H. H. Knight); author's collection. *Allotype*: same data as the type. *Paratypes*: 3♂ 16♀ taken with the types on beech, within leaves rolled by *Phyllaphis fagi* Linnaeus. NEW YORK,—2♀ July 8, 3♀ July 24, Ithaca; ♀ June 30, ♂ 3♀ July 5, 2♂ July 6, ♀ July 9, 3♀ July 14, ♂ July 15, 1♂ 1♀ July 22, ♂ July 25, ♂ Aug. 2, ♂ Aug. 3, Batavia (H. H. Knight).   ♂ June 28, ♀ July 3, ♂ 3♀ July 15, Staten Island (Wm. T. Davis). 3♀ July 23, Staten Island (C. E. Olsen). MASSACHUSETTS,—2♂ 1♀ Aug. 8, Chester (C. W. Johnson). MICHIGAN,—1♂ 1♀ July 8, Holland (A. B. Walcott). NEW JERSEY,—♀ July 2, Jamesburg (Wm. T. Davis). OHIO,—♀ July 20, Columbus (E. Liljeblad). QUEBEC, CANADA,—♀ July 14, Montreal; ♀ July 30, Bondville (G. A. Moore).

This particular variety and only this form was found associated with and predaceous upon *Phyllaphis fagi* Linnaeus on the beech *(Fagus grandiflora),* an aphid which rolls the leaves under tightly from the margin. Specimens of *castus* were taken at Batavia on apple trees with the typical *fasciolus,* which would indicate that both forms may occur in the same situation.

Deraeocoris grandis (Uhler)

1887 *Camptobrochis grandis* Uhler, Ent. Amer. ii, p. 230.

Length 6.4-7 mm. Distinguished by the long rostrum which reaches upon the second segment of the venter; dorsum rather uniformly dark brown, median line of pronotal disk rather broadly but only slightly paler than behind the calli; legs pale, apical half of hind femora and the basal half of tibiae biannulate with blackish.

♂. Length 6.4 mm. *Head*: width 1.03 mm., vertex .49 mm., length .67 mm., in profile more pointed, the base of tylus less prominent than in *borealis,* otherwise very similar in structure; yellowish brown, spot each side of vertex, irregular spots each side of median line, two longitudinal lines and base and apex of tylus, above and below base of antenna, bucculae and to some extent on juga and lorae, dark brownish to black. *Rostrum,* length 2.97 mm., reaching upon second segment of the venter, yellowish brown, darker at base and apex.

Antennae: segment I, length .52 mm., yellowish, becoming darker each side at base; II, 1.74 mm., yellowish, darkened on the apical one-third, scarcely equaling the thickness of segment I, tapering on basal one-third to slender at base, coarsely pubescent, a few exserted hairs nearly equal to twice the thickness of the segment; III, .72 mm., infuscated, yellowish toward base; IV, .51 mm., infuscated, slightly paler at base; the last two segments slender, several exserted hairs equal to twice the thickness of the segment.

Pronotum: length 1.42 mm., width at base 2.39 mm., anterior angles .97 mm.; collar .77 mm., dark brownish, opaque; disk moderately convex, coarsely black punctate, lateral margins slenderly carinate, slightly sulcate on the basal half, anterior angles narrow and rounding to the collar; calli slightly convex, smooth and shining, two punctures between at the median line, delimited behind by coarse punctures, black, yellowish brown just before on the median line; disk brownish to dark brown, usually slightly paler on the central area, the median line appearing broadly paler; propleura punctate, dark brownish, only slightly paler at the margins; xyphus nearly flat, fusco-brownish, coxal margins prominently carinate. *Scutellum* convex, smooth and shining, dark brown; basal angles, apex, median line on apical half, pale; mesoscutum dark brown, slightly paler at middle. *Sternum* dark brown to blackish, opaque except spot at dorsal margin of the meso- and meta-episterna; ostiolar peritreme pale, slightly infuscated at the dorsal margin.

Hemelytra: width 2.9 mm., structurally nearly as in *borealis*; brownish to dark brown, punctures black, paler parts as on embolium and small spot at base of corium stained with brownish. *Cuneus* pale and stained with brownish, apex and narrowly ·at base dark brownish, punctures black. *Membrane* uniformly pale fumate on the apical half; brachium, within the cells and slightly invading the membrane posteriorly, blackish.

Legs: legs pale, hind femora with two fuscous annulations on the apical half; tibiae banded with fuscous on the basal half, the middle and front pair distinctly annulated in darkest specimens; tarsi blackish at tips, claws stained with brownish, structure of the claws and arolia similar to *borealis*.

Fig. 9. *Deraeocoris grandis*, male genital claspers. a, left clasper, lateral aspect; c, right clasper, lateral aspect.

Venter: dark brownish to blackish, shining, clothed with rather long pale yellowish pubescence; genital claspers (fig. 9) distinctive of the species, the base of the left clasper prominent but not produced into a horn.

♀. Length 6.8 mm., width 3.1 mm.; general coloration nearly identical with the male, usually slightly larger in size; segment II, length 1.88 mm., slender, becoming gradually thicker from the base toward apex, not equaling the thickness of segment I, coarsely pale pubescent, a few hairs longer but scarcely equal to twice the thickness of the segment, yellowish, the apical one-fourth brownish black, the last two segments yellowish brown.

Plesiotype: ♂ July 14, Batavia, New York (H. H. Knight); compared with type; author's collection. *Allotype*: same data as the plesiotype. *Specimens examined*: NEW YORK,—♂ July 7, 10♂ 6♀ July 14, 1♂ 1♀ July 31, Batavia; ♀ July 16, Conesus Lake; ♂ June 30, Ithaca (H. H. Knight). ♀ August, West Hebron. ♀ June 19, ♂♀ July 3, White Plains (Torre-Bueno). 1♂ 1♀ July 24, Rockaway Beach, L. Is. (C. E. Olsen), collected in washup. ILLINOIS,—♂ May, "Ill." (C. A. Hart). MARYLAND,—1♂ 1♀ June 14, Beltsville (W. L.

McAtee). MASSACHUSETTS,—♂ July 18, Beach Bluff (H. M. Parshley). ONTARIO, CANADA,—♂ "Grimsby" (J. Petit).

In describing *grandis,* Uhler had under observation at least four different species and made allowance to cover all the forms he had seen of what he took to be merely variations. Nearly every species collected from the United States that is larger than *nebulosus* has at one time or another stood under that name. This condition doubtless resulted from the fact that in the past a hand lens furnished the only means of magnification for the study of specimens. Before the advent of the binocular microscope it was probably not even suspected that so many species of Deraeocoris could exist and yet be so similar in general appearance.

The writer has recently received from the National Museum through the kindness of Mr. E. H. Gibson and later by assistance of Miss Emma Wells, all the specimens from the Uhler collection that stood under the name *Camptobrochis grandis.* There are nine specimens and one pin upon which the specimen has been destroyed. The writer finds this material to be composed of the following : *Deraeocoris nitenatus,* ♂ Aug. 12, 1898, Madison, N. J., ♀, "Pa. 2151"; *D. fulvescens* (Reut.), ♀ May 8, Las Vegas, N. Mex. (Barber & Schwarz) ; *D. nigritulus,* ♀, District of Columbia (Pergande) ; *D. grandis* (Uhler) ♀, "Grimsby" [Doubtless : Grimsby, Ontario, Can., (J. Petit)], no date but identification label and locality in Uhler's handwriting; *D. aphidiphagus* n. sp., ♀ July 15, 1893, Glen Echo, Md.; *Lygus pratensis oblineatus* (Say), ♀ June 6, 1892, "Banft Sp Alb"; *D. barberi* n. sp., ♀ Aug. 13, Las Vegas, N. Mex. (H. S. Barber), labeled *"Camptobrochis grandis* var."; *D. borealis* (Van D.), ♀ Aug. 28, 1888, Marquette, Mich.; one pin with specimen destroyed, June 6, 1893, Glen Echo, Md.

The composite species, *grandis* Uhler, was described early in 1887 and the material from which the description was drawn must have been collected not later than 1886. In the Uhler collection the only possibility for a type is the specimen from "Grimsby" Ontario, Can. (J. Petit) without date, and judging by the age of the name label, in Uhler's handwriting, it must be the only specimen saved from those which served for the description of 1887. Since this specimen appears to be the only possible choice it seems advisable to designate it as the type. In reality the species is distinguished in the original description . from the several closely related species, some of which were likewise included in the description, only by the long rostrum "reaching behind the posterior coxae," and the large size. Several

species were regularly determined as *grandis* by Uhler as witnessed by the above list found in the collection of that author. The writer's determinations for *grandis* until 1920, when the type was recognized, refer to two species, either *borealis* Van D. or *fasciolus* new species.

Lectotype: ♀, "Grimsby" [Ontario, Canada (J. Petit)]; Cat. No. 22684, U. S. N. M.

The writer took all his specimens on hickory *(Carya sp.)*, to which plant the species appears to be confined in its breeding habits. At Batavia, all the specimens were collected on young hickory trees, the first adult being taken on July 7, at which time several nymphs were found. The species is doubtless predaceous to a large extent as indicated by the fact that no injury to foliage was noted and specimens were not numerous on the most favorable growth of hickory. Specimens were scarce on July 31 and the disappearance of the species thereafter indicates that the winter season is passed only in the egg stage.

Deraeocoris betulae new species

Brown to dark brown or blackish, venter dark reddish brown to chestnut red; femora uniformly blackish on the apical half, tibiae triannulate with blackish.

♂. Length 6.7 mm. *Head*: width 1.12 mm., vertex .54 mm., length .63 mm., tylus more prominent at base than in *borealis;* black, shining, in paler specimens the base of vertex, each side of front, spot at base of juga, paler; carina not evident, base of vertex delimited by a groove which separates it from the broadly exposed, black and shining collum. *Rostrum*, length 2.25 mm., reaching to near hind margins of the middle coxae, black, slightly paler at the joints.

Antennae: segment I, length .55 mm., II, 1.77 mm., nearly cylindrical, about equal to segment I in thickness, more slender on the basal one-fourth and slightly so at apex, dusky pubescent, exserted hairs not equal to twice the thickness of segment; III, .77 mm.; IV, .54 mm.; black, base of segment III narrowly brownish, the last two segments slender, beset with fine pale hairs which in length are equal to more than twice the thickness of segment.

Pronotum: length 1.48 mm., width at base 2.48 mm., anterior angles 1.03 mm.; collar .8 mm., brownish black, opaque; disk moderately convex, shining, coarsely and somewhat longitudinally strigate-punctate, more finely punctate near the basal margin, lateral margins distinct, straight, slightly rounded at the anterior angles; brownish black to black, calli smooth, confluent, extending forward to the constriction; propleura more finely punctate than the disk, brownish black, paler at the lower margins; xyphus convex in front, depressed behind, margins carinate at the coxal margin, pale to brownish, or fuscous. *Scutellum* impunctate, convex and shining, dark brownish to black, basal angles and apex paler. *Sternum* brownish black, opaque; ostiolar peritreme pale to brownish, becoming blackish at the dorsal margin.

Hemelytra: width 3.1 mm., structurally very similar to *fasciolus;* rather uniformly dark brownish or brownish black. *Cuneus* brownish black, punctures evident, slightly paler and translucent on the central area. *Membrane* strongly infuscated, a transverse pale area behind the areoles but usually interrupted at middle; the large fuscous spot occupying the apical half irregularly transverse at base, not so clearly rounded at the sides as in the case of *fasciolus.*

Legs: black, apical half of coxae, trochanters, and bases of femora more or less pale; tibiae black, paler at knee, annulus at middle of basal half and a much broader one just beyond middle of tibiae, pale; tarsi black, the second segment and base of third frequently paler; claws brownish to blackish, arolia slender, translucent, bristle-like, nearly parallel but converging slightly at apices.

Fig. 10. *Deraeocoris betulae*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, dorsal and lateral aspect.

Venter: dark reddish brown to chestnut red or mahogany and piceous, shining, yellowish pubescent; genital claspers (fig. 10) distinctive of the species.

♀. Length 7 mm., width 3.2 mm.; usually somewhat paler in color than the male; front of head largely brown but with black spots each side of the median line. *Antennae*: segment I, black; II, 1.85 mm., slender, gradually enlarged toward apex, yellowish, the apical one-fourth black; the last two segments yellowish, darkened with fuscous apically. *Pronotum*: rich brownish to dark brown, calli black, lateral margins of disk slightly sulcate. *Scutellum* brown, becoming blackish each side of the median line. *Venter*: dark reddish or reddish brown, shining, frequently blackish surrounding the spiracles and at base of ovipositor.

Holotype: ♂ July 2, Ithaca, New York (H. H. Knight); author's collection. *Allotype*: taken with the type. *Paratypes*: 20♂ 21♀ taken with the types on *Betula lutea,* the large tree standing about forty feet up behind the Cornell University hydraulic laboratory. CONNECTI-CUT,—♀ July 2, New Haven (W. E. Britton). ♀ July 4, South Meriden (H. Johnson). MAINE,—♀ July 16, Wales (C. A. Frost). ♀ July 24, ♀ July 30, ♀ Aug. 4, Peaks Island (G. A. Moore). 3♂ 1♀ August, Mt. Katahdin, alt. 3,000 ft. (H. G. Barber). MASSACHU-SETTS,—2♂ 1♀ July 18, Beach Bluff (H. M. Parshley). NEW HAMPSHIRE,—♀, Mount Washington; ♂, Franconia (Mrs. A. T. Slosson). NEW JERSEY,—♀ July 4, Hopatcong (H. G. Barber). ♀ July 6, Newfoundland (Wm. T. Davis). NEW YORK,—♂ June 23, 4♂ 2♀ June 30, 1♂ 1♀ July 2, Ithaca (H. H. Knight), on *Acer spicatum.* 2♂ 1♀ June 26, 3♂ 5♀ July 13, Ringwood, near Ithaca; 4♂ 5♀ July 3, McLean Bogs; 2♂ 4♀ July 4, Four Mile (H. H. Knight), all on *Betula lutea.* ♀ June 9, ♀ July 16, Staten Island; ♂ June 20,

Roseville; 2♀ Hamilton County; ♂ July 9, Whiteface Mt. (Wm. T. Davis). ♀ June 28, 5♂ 6♀ July 2, ♂ July 8, White Plains (J. R. Torre-Bueno). ♂ June 20, Ft. Montgomery (F. M. Schott). PENN-SYLVANIA,—♂, Delaware Watergap (Mrs. A. T. Slosson).

Breeds chiefly on yellow birch, *Betula lutea,* the types and a good series being taken from one large tree, mostly from among clusters of aphid-deformed leaves. Nymphs as well as adults were taken on mountain maple, *Acer spicatum,* on the south shore of Beebe Lake, but collecting on the same plant at other localities failed to produce additional records. Caged specimens fed on sap of the host plant, altho observations made in the field point toward predaceous habits also.

Description of the fifth nymphal stage: ♀. Length 5.1 mm., greatest width 2.45 mm., more or less covered with a white, wax-like, flocculent material. *Head*: width 1.14 mm., vertex .65 mm., length .71 mm.; more flattened and eyes smaller than in the adult, vertex, front, and tylus beset with large stiff black bristles; pale testaceous and tinged with pink, eyes darkened. *Rostrum,* length 1.98 mm., reaching to middle of the hind coxae, pale, blackish apically.

Antennae: segment I, length .4 mm.; II, 1.31 mm., more slender than segment I, slightly thickened toward apex, rather sparsely beset with black bristles which in length are equal to twice the thickness of segment; III, .63 mm.; IV, .57 mm.; uniformly dusky or fuscous, the last two segments sparsely beset with hairs.

Pronotum: length .83 mm., width at base 1.57 mm.; anterior angles 1.03 mm., nearly in contact with eyes, front margin sulcate; basal margin nearly straight, rounded at basal angles, lateral margins distinct, nearly straight; disk slightly convex, sparsely beset with coarse black bristles, more prominent at anterior angles; propleura nearly vertical, coxal cleft prominent, xyphus convex, margins ecarinate; testaceous or dusky, darker on disk, the median line paler and continued upon the mesonotum. *Mesonotum* and wing-pads dusky, the latter darker toward apices, both pairs reaching to base of third tergite, sparsely beset with black bristles, larger at the lateral margins.

Legs: pale to reddish brown; femora reddish brown to blackish on the apical half, dusky or paler toward the base, dorsal surface beset with several stiff bristles; tibiae reddish brown to blackish, darkest specimens with an indistinct pale annulus on apical half, anterior surface with two rows or series of stiff bristles; tarsi two-segmented, blackish, claws blackish, arolia similar to those of the adult.

Abdomen: distinctly pink, paler at the margins, ten segments visible from the dorsal aspect, sparsely beset with bristles ranged in rows; third tergite with a dark median spot which also invades slightly the fourth tergite, darkest color inclosing two pore-like spots situated at the suture between the tergites; a row of dark spots situated each side on the submarginal area, a spot at the anterior margin of each tergite and becoming progressively larger distally; eight sternites visible, a spiracle situated each side in the sublateral area of the first seven; last two sternites infuscated along the median line, a longitudinal suture visible which is more evident on the last segment and appears

somewhat cleft at apex. In the male nymph the tip of the genital segment is less symmetrical, not cleft, the tip twisting slightly to one side and usually exposing a small chitinous blade, evidently the beginning of the left genital clasper.

Deraeocoris alnicola new species

General aspect very suggestive of *borealis* but distinguished by the genital claspers, prominent exserted hairs on antennae, and by paler infuscation of the membrane which does not form a distinctly rounded spot on the apical half.

♂. Length 6.5 mm. *Head*: width 1.08 mm., vertex .46 mm., length .57 mm.; structurally as in *borealis;* black, vertex, more or less each side of front, sides on basal half of tylus, gula, genae except spot beneath antenna, bucculae, lower margin of lorae, and narrow tip of tylus, pale to yellowish. *Rostrum,* length 2.17 mm., reaching to near posterior margins of middle coxae, yellowish brown, becoming piceous toward apex.

Antennae: segment I, length .45 mm., black; II, 1.6 mm., black, pale on the basal one-fifth, pale pubescent, exserted hairs long, some equal to three times thickness of segment; III, .63 mm., blackish, paler at base; IV, .48 mm., blackish.

Pronotum: length 1.42 mm., width at base 2.28 mm., anterior angles .97 mm., collar .74 mm.; calli black, invaded by pale at the antero-lateral angles each side of a black lunate mark which extends to anterior angle of disk; a broad widening piceous or black ray behind each callus, usually extending to basal margin of disk, the median line and basal margin narrowly, and the lateral margins more broadly, pale; propleura not so closely punctate as in *borealis,* yellowish brown, blackish surrounding top of coxal cleft. *Scutellum* impunctate, pale, a piceous vitta beginning at base and extending each side of median line to near apex. *Sternum* opaque, brownish black, paler at median line and margins; pleura dark brownish, paler at margins, basalar plate yellowish; ostiolar peritreme pale, darkened with brownish above. .

Hemelytra: width 2.77 mm., structurally as in *borealis* but more broadly piceous on corium and apical half of embolium. *Cuneus* pale, punctures evident but blackish only at base, apex more broadly black than in *borealis. Membrane* pale, the apical half infuscated but not heavily so, the infuscation not rounded at sides but rather transverse at base, leaving an irregular transverse paler streak across middle of membrane; apical half of areoles and veins infuscated, a distinctly darker mark paralleling the brachium at apex of larger areole.

Legs: pale testaceous, apical half of femora blackish, forming two paler bands near apex; tibiae triannulate with blackish, in pale forms the apices paler; tarsi, claws and arolia as in *borealis.*
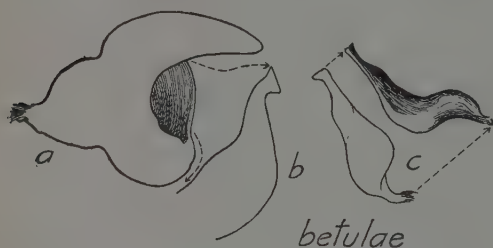

Fig. 11. *Deraeocoris alnicola,* male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: piceous, shining, pale yellowish pubescent; genital claspers (fig. 11) distinctive of the species, the left clasper with a prominent horn at base.

♀. Length 6.5 mm., width 2.9 mm.; general coloration similar to the male but slightly paler, usually with less piceous on the hemelytra, scutellum, and front of head; seg-

ment II, length 1.62 mm., slender, slightly thicker at apex, beset with prominent exserted hairs which in length are equal to three times thickness of segment, yellowish, usually darker at apex and sometimes slightly dusky near base; segment I paler at apex while the last two segments are paler than in the male; venter reddish to brownish and rarely with some piceous; apices of tibiae usually paler than in the male.

Holotype: ♂ July 3, McLean, New York (H. H. Knight); author's collection. *Allotype*: same data as the type. *Paratypes*: 30♂ 28♀, taken with the types on alders, *Alnus incana,* growing along the stream which flows out from the bogs. CONNECTICUT,—2♂ 3♀ June 19, Wallingford (J. D. Caffrey). ♂ June 20, New Haven (B. H. Walden). ♀ July 2, New Haven (W. E. Britton). 1♂ 1♀ July 3, Stonington (I. W. Davis). NEW YORK,—♂ 2♀ June 24, 2♀ July 5, Batavia; 2♀ June 27, Portage; ♀ July 27, McLean (H. H. Knight). 2♂ June 24, 2♂ 2♀ June 30, ♂ July 2, ♀ July 6, 2♂ 6♀ July 7, White Plains (J. R. Torre-Bueno). ONTARIO, CANADA,—3♂ July 1, Ottawa (H. G. Crawford). ♂ June 19, Hastings County (Evans).

The writer found this species only on alders, *Alnus incana,* but not in the same situations with *borealis.* On one occasion an adult bug was discovered feeding on a small adult Fulgorid, *Lamenia vulgaris* Fitch. Aphids and Psyllids were very abundant on the alders where *alnicola* was taken and both nymphs and adults doubtless feed to a considerable extent on these small insects.

Deraeocoris shastan new species

General aspect very similar to *alnicola* but the median line of pronotal disk not clearly defined with pale, disk more closely and finely punctate, abruptly convex at lateral margins, bucculae black while the juga are chiefly pale.

♀. Length 6.5 mm. *Head*: width 1.11 mm., vertex .55 mm., length .63 mm.; nearly as in *alnicola,* but genae broader and more tumid, front and vertex slightly more convex; pale to yellowish, black bars and spots each side of median line of front, black on the impressed spot at each side of vertex; base and two vittae on basal half of tylus, bucculae, dorsal margin of lorae, beneath base of antenna and more or less at apex of tylus, blackish, juga pale or only slightly dusky on its convexity. *Rostrum,* length 2.28 mm., reaching to near hind margins of middle coxae, yellowish brown, apex piceous; basal segment just attaining base of head, a black line each side of the suture.

Antennae: segment I, length .5 mm., brownish to fuscous; II, 1.48 mm., slender at base, tapering gradually to thicker at apex but not equaling the thickness of segment I, beset with several exserted pale hairs, the length of some equal to three times thickness of segment, fusco-brownish, slightly paler at extreme tip; III, .63 mm.; IV, .49 mm.; last two segments brownish to black.

Pronotum: length 1.4 mm., width at base 2.31 mm., anterior angles 1.11 mm., collar .85 mm.; lateral margins slenderly carinate, slightly sulcate, disk

abruptly convex from the lateral margin, central area somewhat flattened; disk more finely and closely punctate than in *alnicola;* calli convex, black, also a lunate mark which extends to anterior angle of disk, brownish black to black behind the calli; brownish on the central area of disk but the median line is not emphasized, lateral margins broadly pale; propleura pale, a blackish spot behind the coxal cleft on the lower half; xyphus yellowish, blackish each side behind the collar. *Scutellum* convex, smooth, somewhat depressed at middle of base, brownish black, basal angles and median line except at base pale. *Sternum* opaque, brownish black, the median line and margins paler; pleura dark brownish to blackish, paler at margins and on basalar plate; ostiolar peritreme pale, invaded with blackish above.

Hemelytra: width 2.9 mm., lateral margins more distinctly arcuate than in *alnicola;* black punctate, clavus brownish to blackish, darker at apex and bordering claval suture on basal half; embolium and lateral margin of corium except apex pale, broadly at apex and more or less connected with spot at middle of corium blackish. *Cuneus* pale, inner basal angle and the apex black-ish. *Membrane* pale, brachium dark brownish, stained with fuliginous at either side, perhaps the apical half somewhat fuliginous in the male or darkest specimens.

Legs: not differing appreciably from those of *alnicola.*

Venter: brownish with blackish, bordering the ovipositor and sutures of the genital seg-

Fig. 12.   *Deraeocoris shastan,* male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

ments, and surrounding 'the spiracles, blackish.

Holotype: ♀ May 28, Siskiyou County, California (F. W. Nunenmacher); author's collection. *Allotype:* May 20, 1920, Bryson. Monterey County, California (E. P. Van Duzee).

This species is named after the Shastan Indians, a tribe that inhabited northern California. The male specimen was received too late to serve for the description. It is slightly smaller than the female but very similar in coloration; genital claspers (fig. 12) distinctive of the species.

Deraeocoris aphidiphagus new species

1909 †*Camptobrochis grandis* Reuter, Acta Soc. Sci. Fenn., xxxvi, No. 2, p. 56.
Fusco-grayish to blackish, the paler and translucent parts not stained with brownish, apical half of membrane infuscated, tibiae triannulate with blackish; left genital clasper having a long horn at the dorsal margin; structurally as in *borealis* unless otherwise described.

♂. Length 5.9 mm. *Head:* width 1.08 mm., vertex .51 mm., length .57 mm.; pale, large spot each side of vertex, four or five transverse marks forming an arc each side of median line and sometimes meeting in front of ver-

tex, triangular spot at base and two longitudinal lines and apex of tylus, above and below base of antenna, gula, bucculae, dorsal margin of lorae, and somewhat on juga, fuscous to black. *Rostrum,* length 2.15 mm., scarcely attaining the posterior margins of the middle coxae, yellowish brown, darker at apex, basal segment blackish each side at middle.

Antennae: segment I, length .48 mm.; II, 1.48 mm., slender at base and gradually thickened toward apex, equaling the thickness of segment I, pale pubescent, length of longest hairs not equal to more than thickness of segment on apical half; III, .63 mm.; IV, .45 mm.; all the segments fuscous to blackish, segment III paler at base.

Pronotum: length 1.42 mm., width at base 2.39 mm., anterior angles 1 mm., collar .8 mm.; disk more closely punctate than in *borealis* or *fasciolus,* punctures delimiting posterior margins of calli more or less confluent, lateral margins slenderly carinate and perceptibly sulcate; calli slightly convex, separated by two closely set punctures at the median line, black, a lunate mark at the antero-lateral angles; grayish testaceous and more or less darkened with fuscous and black, the median line and the sublateral area of disk usually slightly paler; propleura blackish, dorsal, posterior and ventral margins more or less pale; xyphus pale to blackish. *Scutellum* smooth, convex and shining, brownish black, basal angles, apex, and median line pale. *Sternum* opaque, black, basalar plate yellowish to brown; ostiolar peritreme pale, becoming blackish above.

Hemelytra: width 2.9 mm., lateral margins very slightly arcuate; grayish translucent and darkened with fuscous and blackish, clavus darker along the sutures and at apex; embolium except at apex, spot at base of corium and bordering the embolium except at apex, pale translucent; spot at middle and more or less broadly on the outer apical area of corium piceous or black, punctures black. *Cuneus* pale translucent, punctures and apex black. *Membrane* pale fumate, apical half usually distinctly infuscated, brachium and more or less invading the membrane each side, fuscous.

Legs: pale, femora biannulate with fuscous or blackish on the apical half, frequently obsolete on the front pair; tibiae triannulate with fuscous or blackish, the apical annulus usually paler; tarsi pale to brownish, infuscated on apices; claws brownish translucent, arolia typical of the group.
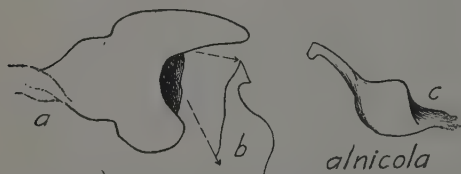

Fig. 13. *Deraeocoris aphidiphagus,* male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: black, shining, sometimes with brownish near lateral margins, pale or yellowish pubescent; genital claspers (fig. 13) distinctive of the species, the long horn at the dorsal margin of the left clasper taken in combination with the comparatively slender internal arm is quite different from any other known species.

♀. Length 6.1 mm., width 3 mm., very similar to the male in structure and coloration; segment II, length 1.51 mm., slender, gradually thickened toward apex, scarcely equal to thickness of segment I, pale

pubescent, the longest hairs equal to little more than thickness of segment.

Holotype: ♂ July 24, Ithaca, New York (H. H. Knight); author's collection. *Allotype*: same data as the type. *Paratypes*: ARKAN-SAS,—2♂ 2♀ May 27, Fayetteville (G. G. Becker). 2♂ 2♀ May 15, 2♂ 1♀ May 20, Siloam Springs. COLORADO,—4♀ July 3, Fort Collins. CONNECTICUT,—♀ June 13, Wallingford (J. K. Lewis). DISTRICT OF COLUMBIA,—♂♀ May 30, 1879, ♂ June, 1885, Washington, "preying upon *Schizoneura americana*" (T. Pergande). ♀ June 10, Washington (O. Heidemann). ♀ June 25, Washington (Wm. T. Davis). ♂ July 6, Washington (W. L. McAtee). ILLINOIS,—3♂ 1♀ July 2, Willow Springs, (W. J. Gerhard). ♂ June 6, Angerville (J. R. Malloch). ♂, "N. Ill." (A. Bolter). ♂ June 16, 1885, Urbana (C. A. Hart). MAINE,—2♀ July 1, ♀ July 11, Orono (E. M. Patch). ♀ August, Mt. Katahdin, alt. 4,300 ft. (H. G. Barber). MARYLAND,—2♂ 3♀ July 15, ♀ Aug. 10, Glen Echo; ♀ June 15, Plummer's Island (O. Heidemann). ♀ June 10, Great Falls (F. Knab). ♀ June 4, Plummer's Island (W. L. McAtee). MICHIGAN,—2♂ 3♀ June 28, 1♀ July 1, Berrien County; ♂ June 18, Ann Arbor (R. F. Hussey). ♀ August, Marquette. MINNESOTA,—14♂ 20♀ June 29, Twin Lake, Martin County; ♂ July 13, St. Anthony Park (H. H. Knight). ♀ July 2, Mille Lacs County (V. R. Haber). ♂ 3♀ July 10, Rush Lake, St. Louis County (W. A. Riley). NEW HAMPSHIRE, —5♀, Fabyan. NEW·YORK,—♂ 3♀ June 16, ♂ July 23, ♀ July 24, 1♂ 1♀ July 26, ♀ July 30, Ithaca; ♂ June 17, 2♂ July 7, ♀ July 12, 4♂ 3♀ July 14, ♀ July 27, Batavia; ♂ July 16, Conesus Lake; 2♀ July 27, McLean; ♂ July 27, Portageville (H. H. Knight). ♂ July 14, Lancaster (E. P. Van Duzee). ♀ July 14, White Plains (J. R. Torre-Bueno). OHIO,—2♂ 1♀ June 21, Mercer County (R. F. Hussey). NORTH DAKOTA,—♀ July 14, Kidder County (A. A. Nichol). SOUTH DAKOTA,—6♂ 4♀ June 30, ♀ July 11, ♀ July 13, ♂ July 15, Brookings (H. C. Severin). VIRGINIA,—1♂ 1♀ June 6, ♀ June 27, Mount Vernon (W. L. McAtee). ♀ May 30, Glen Carlyn (D. H. Clemens). ♂ July 7, Rosslyn (O. Heidemann). CANADA: ONTARIO,—♂ June 24, Trenton (Evans). ♂ July 6, Ottawa (J. Fletcher). NOVA SCOTIA,—2♂ 1♀ July 31, Truro (E. C. Allen). QUEBEC,—♀ July 13, Bord-a-Plouffe (G. A. Moore).

The writer has found this species breeding only on the elm *(Ulmus)* and in the curled leaves infested with *Schizoneura americana* Riley. Both nymphs and adults feed on the aphids and their honeydew excretions. The nymphs are coated with a white, wax-like material similar to that which covers the aphids, and in the early stages at

least are rather inconspicuous, as they live among the aphids and their excretionary products. The eggs are doubtless deposited during July in the twigs or buds, where they pass the winter, and upon hatching in the spring the young nymphs seek out the aphid-infested leaves very soon after the leaves are curled. In the writer's experience *aphidiphagus* was found closely associated only with *Schizoneura americana* but extended observations may show that other elm aphids are fed upon when the preferred species is not to be had.

Mr. Van Duzee writes that this species is the form which Reuter (1909) took to be *Camptobrochis grandis* Uhler and that he also has looked upon *aphidiphagus* as representing that species. The writer would call attention to the fact that until the present time the references to *grandis* Uhler refer to a group of species, as witnessed by numerous determinations examined, and should be accepted only with this in mind.

Deraeocoris triannulipes new species

Closely related to *aphidiphagus* but darker colored and the paler parts stained with brownish; genital claspers distinctive, the internal arm of the left clasper very different from that in *aphidiphagus*.

♂. Length 6.4 mm. *Head*: width 1.06 mm., vertex .54 mm., length .62 mm.; very similar to *aphidiphagus* but more broadly blackish at base of tylus and lower part of front, also blackish along front margin of eyes. *Rostrum*, length 1.99 mm., reaching to middle of intermediate coxae, yellowish brown, darker at apex.

Antennae: segment I, length .45 mm., fuscous to blackish; II, 1.51 mm., more slender on the basal half, the apical half scarcely equaling the thickness of segment I, pale pubescent, the length of a few exserted hairs slightly exceeding the thickness of segment, brownish black, paler on the basal one-third; III, .68 mm.; IV, .6 mm.; last two segments slender, brownish black, segment III paler at base.

Pronotum: length 1.34 mm., width at base 2.42 mm., anterior angles 1.03 mm., collar .8 mm.; uniformly brownish black, basal and lateral margins slenderly pale, brownish at the median line before the calli; xyphus and lower margins of propleura pale, fuscous mark each side at anterior angles of xyphus. *Scutellum* brownish black, basal angles, apex and a slight indication on median line pale; mesoscutum dark brownish. *Sternum* and pleura dark brownish black, basalar plate slightly paler; ostiolar peritreme pale, slightly darkened at dorsal margin.

Hemelytra: width 2.85 mm., nearly as in *aphidiphagus;* brownish black, basal half of embolium, spot at base of corium, and more or less on clavus, pale brownish translucent, the paler parts distinctly stained with brownish. *Cuneus* brownish black, more or less pale translucent at middle, the punctures dark. *Membrane* pale brownish or fumate, veins slightly darker, basal half of the larger areole and a spot at each side by apex of cuneus paler.

Legs: pale, femora more or less brownish black on the apical half, a pale band just before apex but interrupted on the anterior face, the basal half with a· linear series of fuscous spots, the anterior pair more broadly pale; tibiae triannulate with brownish black, also with a spot at knee; tarsi yellowish brown, darker at apices, claws and arolia typical of the group.
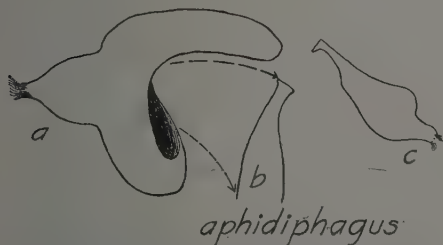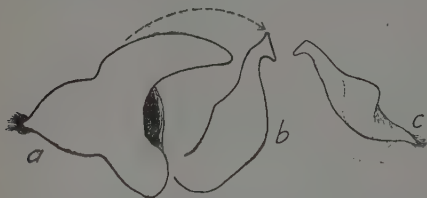

Fig. 14. *Deraeocoris triannulipes,* male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: black or brownish black, pale pubescent; genital claspers (fig. 14) distinctive of the species.

Holotype: ♂ Aug. 2, Rico, Colorado (E. D. Ball); author's collection. *Paratype*: ♂ Aug. 8, Husavick, Manitoba (Coates); collection of E. P. Van Duzee.

Deraeocoris quercicola new species

Darker colored than *nitenatus,* fuscous to blackish, calli black, apical half of membrane fumate, rarely so pale as in *nitenatus;* left genital clasper with a long dorsal horn which is very distinctive when taken in consideration with the form of the internal arm.

♂.· Length 5.5 mm. *Head*: width .98 mm., vertex .45 mm., length .57 mm., structurally nearly as in *borealis;* pale to yellowish, collum, spot each side of vertex, arc each side of front composed of transverse bars and practically joining above, above and' below base of antenna, geminate mark on tylus with spot at base and slightly at apex, bucculae and more or less on juga and lorae, black or brownish black. *Rostrum,* length 1.98 mm., attaining posterior margins of middle coxae, pale to brownish, darker at apex.

Antennae: segment I, length .46 mm., pale, darkened slightly with fuscous on basal half; II, 1.54 mm., nearly cylindrical, about equal to segment I in thickness, more slender on the basal one-fifth and very slightly so at tip, brownish, paler at base and brownish black on the apical one-fourth, pale pubescent, length of a few exserted hairs exceeding thickness of segment; III, .65 mm.; IV, .48 mm.; last two segments yellowish brown, becoming infuscated apically.

Pronotum: length 1.2 mm., width at base 1.99 mm., anterior angles .91 mm., collar .68 mm.; disk rather uniformly black punctate, lateral margins distinct, slenderly carinate, perceptibly sulcate, anterior angles slightly rounded; brownish black, frequently rather broadly paler along median line and on the lateral submarginal area; calli slightly convex, smooth and shining, black, pale just before but the dark color extending from the antero-lateral angles to front margin of disk, separated at base by a pair of punctures at median line; propleura brownish black, lower margin paler; xyphus convex anteriorly, pale, disk darkened with brownish or fuscous. *Scutellum* convex, smooth and shining, basal angles, apex and frequently the median line pale. *Sternum* and pleura brownish black, opaque, basalar plate more brownish; ostiolar peritreme white.

Hemelytra: width 2.4 mm., black punctate, moderately convex, lateral mar-

gins slightly sinuate; brownish black to piceous, darkest at middle and on outer apical half of corium; embolium except apically, spot at base and inner apical angles of corium, and clavus largely, pale brownish translucent. *Cuneus* pale translucent, punctures black, apex broadly blackish. *Membrane* pale to fumate, slightly paler bordering tip of cuneus, veins brownish to fuscous, the dark color invading the membrane slightly at each side.

Legs: pale, hind femora with two blackish marks on the dorsal surface near apices; tibiae devoid of infuscations; tarsi infuscated at tips, claws and arolia typical of the group.

quercicola

Fig. 15. *Deraeocoris quercicola,* male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: brownish black, shining, pale pubescent; genital claspers (fig. 15) distinctive of the species.

♀. Length 5.8 mm., width 2.82 mm., very similar to the male but slightly more robust, usually paler in color; calli black, disk of pronotum usually more brownish than blackish; scutellum sometimes only brownish but typically with a blackish vitta each side of median line; corium dark brownish to piceous on the middle and outer apical area; segment II, length 1.57 mm., slender, gradually thickened toward apex, pale or yellowish, becoming brownish at apex; femora frequently with only a brown mark on apical half.

Holotype: ♂ July 16, Conesus Lake, New York (H. H. Knight); author's collection. *Allotype*: same data as the type. *Paratypes*: 8♂ 5♀, taken with the types on *Quercus alba*. COLORADO,—♂ June 30, Fort Collins; ♀ July 19, Colorado Springs (E. D. Ball). CONNECTICUT,—2♂ July 8, New Haven. ♂ July, East River (C. R. Ely). DISTRICT OF COLUMBIA,—♀ June 22, Washington (Wm. T. Davis). ♀ July 2, Washington (O. Heidemann). GEORGIA,—1♂ 1♀ Clayton, alt. 3,000 ft. (Wm. T. Davis). ILLINOIS,—♂ June 3, ♀ June 8, ♀ July 9, Chicago; ♂ June 19, Glen Ellyn; ♂ June 24, Willow Springs (W. J. Gerhard). ♂ June 12, ♂ June 15, Champaign (C. A. Hart). ♀ July 6, Elizabeth (J. R. Malloch). INDIANA,—♀ June 9, Harrison County (H. F. Dietz). KANSAS,—♂ June, Lawrence (E. S. Tucker). MASSACHUSETTS,—♂ June 30, Arlington (G. W. Barber). ♀ June 26, Newton. ♂ July 16, Beach Bluff, ♀ July 28, Pigeon Cove (C. E. Olsen). ♂ July 18, Beach Bluff (H. M. Parshley). MICHIGAN,—3♀, "Mich." (Uhler collection). MINNESOTA, —♂♀ June 29, Twin Lake, Martin County (H. H. Knight). NEW JERSEY,—♀ July 25, Bear Swamp, Ramapo Mts. (Wm. T. Davis). ♀ July 4, Hopatcong; ♀ July 20, 7♀ July 25, ♀ July 27, Bear Swamp, Ramapo Mts. (H. G. Barber). NEW YORK,—1♂ 1♀ July 4, 2♂ July 5, Batavia; 2♂ July 4, Four Mile; ♂ June 21, 5♂ 2♀ June 27,

Portageville; 2♂ June 19, ♀ July 2, ♀ July 23, Ithaca (H. H. Knight). 1♂ 1♀ July 11, Massapegua, Long Island; ♀ July 7, Roseville; 2♂ June 21, Richmond; ♀ July 1, ♀ July 5, ♀ July 25, Staten Island; 2♂ June 19, 2♀ June 20, Pine Island (Wm. T. Davis). 2♂ July 2, 4♀ July 6, 2♀ July 18, White Plains (J. R. Torre-Bueno). 1♂ 2♀ July 4, Bayshore; 1♂ 3♀ July 4, Yaphank (C. E. Olsen). NORTH CAROLINA, —♀ June 25, Black Mts. (Beutenmuller). NEW MEXICO,—2♂ 1♀ July 12, 3♂ 2♀ Aug. 1, Jemez Springs, alt. 6,400 ft. (J. Woodgate). PENNSYLVANIA,—2♂ 1♀ Delaware Watergap (Mrs. A. T. Slosson). ♀, Jeannette (H. G. Klages). WISCONSIN,—1♂ 1♀ June 23, Beaver Dam (W. E. Snyder). CANADA: ONTARIO,—♂ "Grimsby" (J. Petit). QUEBEC,—♀ July 13, Bord-a-Plouffe (G. A. Moore).

Deraeocoris quercicola pallens new variety

♂♀. Structurally nearly identical with the typical *quercicola* but differs in color characteristics as follows: front of head pale or with the dark spots much reduced; calli frequently with pale on the disk of each, pronotal disk rather uniformly colored; scutellum pale, rarely with some blackish each side of the median line; hemelytra pale to yellowish, corium with a spot at middle, small one at base, and irregularly at apex, blackish.

Holotype: ♂ Aug. 12, Batavia, New York (H. H. Knight); author's collection. *Allotype*: same data as the type. *Paratypes*: 2♂ 7♀ taken with the types on *Quercus macrocarpa*. COLORADO,— ♀July 19, Colorado Springs (E. D. Ball). MINNESOTA,—3♂ 5♀ June 18, 2♂ 3♀ June 21, 4♀ Aug. 11, St. Anthony Park; 2♀ July 20, Gray Cloud Island; ♂ 6♀ Twin Lake, Martin Co. (H. H. Knight). NEW MEXICO,—3♀ Aug. 1, Jemez Springs (J. Woodgate). NEW YORK,—♂ July, 1886, Buffalo (E. P. Van Duzee). ♂ 4♀ July 4, 3♀ July 12, ♂ July 13, ♂ 3♀ July 14, Batavia (H. H. Knight).

Apparently only a color variety of *quercicola* but one which the writer has found rather consistently on *Quercus macrocarpa*. The color pattern is fixed shortly after the adult emerges and is retained throughout the life of the insect. Tenerel forms of the typical species pass through the color stage represented by *pallens* but when allowed to live, the darker colors are developed and fixed within a few hours after emergence.

Deraeocoris davisi new species

Slightly smaller than *nitenatus*, uniformly brownish black, legs and antennae chiefly pale; genital claspers very distinctive, nearest to *quercicola* but the internal arm of the left clasper more highly developed.

♂. Length 5.3 mm. *Head*: width 1.01 mm., vertex .43 mm., length .54 mm.; brown and marked with brownish black, dark markings similar to those of *quercicola* except that the blackish color each side of front is not broken into transverse bars. *Rostrum*, length 1.92 mm., nearly attaining the posterior margins of middle coxae, yellowish brown, darker at apex.

Antennae: segment I, length .45 mm., yellowish, darker on ventral side of basal half; II, 1.37 mm., equal in thickness to segment I, slender at base, tapering slightly at apex, pale pubescent, length of exserted hairs exceeding thickness of segment, yellowish, becoming brown on the middle one-third; III, .54 mm., yellowish, fuscous toward apex; IV, .43 mm., fuscous.

Pronotum: length 1.22 mm., width at base 2.11 mm., anterior angles .94 mm., collar .73 mm., brownish black, opaque; disk closely punctate, more coarsely behind the calli, lateral margins slenderly carinate, nearly straight, anterior angles gently rounded; uniformly brownish black, calli and anterior portion slightly darker, slender basal margin slightly pale; propleura with ventral and posterior margins paler, xyphus yellowish. *Scutellum* convex, smooth and shining, deep brownish black, small spot at tip and narrowly at basal angles, yellowish brown. *Sternum* dark brownish to blackish, paler at the median line; ostiolar peritreme pale to yellowish.

Hemelytra: width 2.51 mm., structurally as in *nitenatus*; brownish black, basal half of embolium and a small spot near base of corium brownish transluscent. *Cuneus* dark brownish, brownish translucent across the middle. *Membrane* nearly as in *nitenatus*, the apical half sometimes very faintly and uniformly stained with brownish, veins and areoles darkened with brownish.

Legs: pale or yellowish, the hind femora marked on the apical half with an incomplete band as in *nitenatus*; tarsi slightly brownish at apices.

Venter: brownish black to piceous, pale yellowish pubescent; genital claspers (fig. 16) very distinctive of the species.
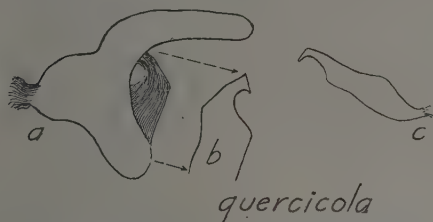

Fig. 16. *Deraeocoris davisi*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Holotype: ♂ June 22, Staten Island, New York (Wm. T. Davis); author's collection. *Paratypes*: ♂ June 18, ♂ June 22, ♂ June 23, Staten Island, New York (Wm. T. Davis). ♂ May 11, Spring Hill, Alabama (H. P. Loding).

Deraeocoris nitenatus new name

1909 *Camptobrochis (Euarmosus) nitens* Reuter, Acta Soc. Sci. Fenn., xxxvi, No. 2, p. 56. (name preoccupied)

1910 *Camptobrochis nitens* Banks, Cat. Nearc. Hem. Het., p. 43.

1916 *Camptobrochis grandis* var. *nitens* Van Duzee, Check List Hemip., p. 41.

1917 *Camptobrochis grandis nitens* Parshley, Occas. Papers Bost. Soc. Nat. Hist., vii, Faun. N. Eng., 14, p. 93.

1917 *Camptobrochys grandis* var. *nitens* Van Duzee, Cat. Hemip., p. 356.

General aspect very similar to *quercicola* but differs as follows: more highly polished, calli black around the margins only, dorsum rich brownish to dark brownish and piceous, frequently brownish on scutellum but rarely blackish each side of median line; brachium and apices of the areoles dark fuscous while the apical half of membrane is practically clear; male genital claspers very distinctive.

♂. Length 5.7 mm. *Head*: width 1.01 mm., vertex .45 mm., length .57 mm.; tylus slightly more prominent but the infuscations are nearly identical with *quercicola*. *Rostrum*, length 1.94 mm., nearly attaining posterior margins of middle coxae, pale yellowish, piceous at apex.

Antennae: segment I, length .48 mm., yellowish, irregularly infuscated on basal half; II, 1.45 mm., yellowish, darkened at apex; III, .68 mm.; IV, .56 mm., comparatively longer than in *quercicola;* last two segments yellowish to fuscous.

Pronotum: length 1.28 mm., width at base 2.2 mm., anterior angles .88 mm., collar .71 mm.; disk more coarsely punctate on the basal half, dark brownish to piceous, darker on the basal half either side of the median line; calli slightly convex, piceous on the front and hind margins, the disk of each paler and connected at the latero-anterior angles with the pale color just in front; propleura closely punctate, yellowish brown, blackish and opaque surrounding the coxal cleft; xyphus pale to brownish. *Scutellum* strongly convex, polished, pale, frequently becoming reddish or brownish each side of the median line, very rarely with blackish. *Sternum* and pleura brownish black, opaque; ostiolar peritreme white.

Hemelytra: width 2.04 mm., structurally as in *quercicola;* apical half of corium and invading the embolium piceous, the clavus and a spot each side of apex on the corium, basal half of embolium, spot near base of corium, pale to brownish translucent. *Cuneus* pale translucent, punctures black, yellowish brown at apex and becoming fuscous at the inner margin where the brachium joins. *Membrane* clear or practically so, brachium and apices of the areoles dark fuscous; apical half of membrane distinctly clearer than in *quercicola.*

Legs: pale, hind femora with a brownish black mark on the anterior face of apical half, sometimes indicated on the middle pair; tips of tarsi fuscous, claws brownish translucent, arolia typical of the group.

Fig. 17. *Deraeocoris nitenatus,* male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: brownish to reddish brown and piceous, shining, finely pale yellowish pubescent; genital claspers (fig. 17) distinctive of the species.

♀. Length 6 mm., width 2.9 mm., very similar to the male but usually more robust; segment II, length 1.51 mm., slender, slightly enlarged on the apical one-fourth, yellowish,

becoming brownish at apex, exserted hairs prominent, in length equal to more than twice greatest thickness of segment.

Plesiotypes: ♂ July 22, Cold Spring Harbor, New York; ♀ Sept. 27, Northampton, Mass. (H. M. Parshley); compared with type; author's collection. *Lectotype*: ♂ June 25, 1904, Washington, D. C. (O. Heidemann); Cat. No. 24169 U. S. N. M. This specimen bears a Reuter label *"Camptobrochis n. sp."* and is the second specimen mentioned under the original description. *Specimens examined*: CONNECTICUT,—♂ Aug. 14, New Haven (W. E. Britton). DISTRICT OF COLUMBIA,—♂ May 11, 2♀ June 28, 3♂ 4♀ June 30, 2♂ 1♀ July 8, 3♀ July 20, 1♂ 1♀ Aug. 2, Washington (O. Heidemann). ILLINOIS,—♂ July 24, Galesburg (Stromberg). MARYLAND,—2♀ June 15, Beltsville (W. L. McAtee). ♂ Aug. 3, Forest Glen; ♂♀ Henson Creek (O. Heidemann). ♀ Sept. 2, Plummer's Island (H. L. Viereck). MASSACHUSETTS,—♀ Sept. 15, Blue Hills; ♂ Sept. 17, Forest Hills; 1♂ 1♀ Sept. 7, Saugus (H. M. Parshley). ♂ July 29, Pigeon Cove (C. E. Olsen). ♀ Aug. 20, Farmington (C. A. Frost). ♂ July 30, Auburndale. 2♂ Aug. 5, Brookline. ♀ Sept. 5, Wood's Hole. MINNESOTA,—2♂ July 20, Gray Cloud Island; 1♂ 1♀ July 29, St. Paul, predaceous on *Schizoneura lanigera,* which makes a rosette gall of elm leaves; 4♂ 8♀ Aug. 5, St. Anthony Park, on *Quercus macrocarpa* (H. H. Knight). NEW JERSEY,—♂♀ July 27, Bear Swamp, Ramapo Mts. (H. G. Barber). NEW YORK,—♂ July 22, ♂ July 26, 2♂ July 29, 2♂ Aug. 4, Cold Spring Harbor (H. M. Parshley). ♂ July 24, ♂ July 29, Ithaca (H. H. Knight). ♂ July 27, Aqueduct; ♀ July 23, 1♂ 1♀ Aug. 1, ♀ Aug. 3, ♀ Aug. 12, Staten Island (Wm. T. Davis). ♀ July 31, Bayshore; ♂ July 18, ♀ Aug. 1, Maspeth; ♀ Aug. 7, Roslyn; ♂ 2♀ July 23, Staten Island (C. E. Olsen). ♂ July 18, 3♀ July 27, 2♂ 1♀ Aug. 14, White Plains (J. R. Torre-Bueno). ♀ July 14, Lancaster (E. P. Van Duzee). NORTH CAROLINA,—♂ June 25, Black Mts. (Beutenmuller). PENNSYLVANIA,—♀ Sept. 8, Central (Wm. T. Davis). ♂ July 5, Harrisburg. ♀ Aug. 6, Twin Lakes (C. L. Pollard). ♂, Delaware Watergap (Mrs. A. T. Slosson). VIRGINIA,—♀ July 30, Great Falls (H. G. Barber). CANADA: QUEBEC,—♂ Aug. 10, Lachine (G. A. Moore).

The writer found this species to be predaceous on *Schizoneura lanigera* (of Patch) which makes a rosette gall of elm leaves. It was, however, never found in company with *D. aphidiphagus* which develops with and is predaceous upon *Schizoneura americana* Riley. Mr. C. E. Olsen states that he also has observed *nitenatus* to be predaceous on elm aphids which formed a rosette gall. Specimens were taken

August 5 by beating the limbs of *Quercus macrocarpa,* and the isolated
occurrence suggests that *nitenatus* is predaceous upon plant lice or
other small soft-bodied insects on that tree. Dr. H. M. Parshley col-
lected adults from among the nymphs of *Corythucha associata* O. & D.
on wild cherry, but the true relationship between the forms was not
determined.

Deraeocoris fulvus new species

Smaller than *nitenatus,* fulvous to piceous, male becoming piceous on pro-
notum and hemelytra, female piceous only at inner apical angles of corium.

♂. Length 4.3 mm. *Head*: width .88 mm., vertex .4 mm., length .43 mm.;
base of vertex slightly elevated to form a carina which extends higher than
the black and broadly exposed collum; luteous to brownish, polished, bordering
inner margins of eyes and extending slightly upon vertex, geminate mark on
basal half of tylus, genae, dorsal margins of bucculae and lorae, somewhat on
juga and the tip of tylus, blackish. *Rostrum,* length 1.48 mm., reaching to near
posterior margins of middle coxae, yellowish, dark brown at apex.

Antennae: segment I, length .34 mm.; II, 1.2 mm., cylindrical, thicker than
segment I, abruptly slender at base and slightly so at apex, pale pubescent,
length of exserted hairs scarcely equal to thickness of segment; III, .44 mm.;
IV, .33 mm.; yellowish, the apex of segment II very little, if any, darker, the
last two segments slightly dusky.

Pronotum: length .97 mm., width at base 1.71 mm., anterior angles .74
mm.; collar 6 mm., dark brown, opaque; punctures concolorous, lateral mar-
gins straight, ecarinate; calli slightly convex, confluent with the apical area of
disk, polished; disk fulvous, anterior part and posterior half becoming piceous,
darkest specimens with only a fulvous spot behind the calli, the slender basal
margin remaining pale or ivory-white; propleura yellowish brown, opaque, coxal
cleft and just above at anterior angle blackish; xyphus slightly convex in front,
receding posteriorly, yellowish to dusky brown. *Scutellum* convex, polished, pale
to yellowish, becoming brownish on disk but apparently never very dark. *Ster-
num* dark brownish, more brownish at the sides and on pleura, basalar plate
pale yellowish; ostiolar peritreme white, sometimes tinged with yellowish, finely
pilose on the episternum just above.

Hemelytra: width 2.02 mm., black punctate, very few punctures on basal
half of embolium; clavus yellowish brown, darker along inner margins and
each side of claval vein; corium dark brownish to piceous, more or less pale
or clear near the basal angle; embolium pale yellowish translucent, somewhat
invaded with piceous near apex. *Cuneus* pale translucent to yellowish on the
basal half, dark fusco-brownish on the apical half, punctures chiefly pale.
Membrane clear or only slightly tinged with yellowish, brachium darkened
with brownish along apex of cells.

Legs: pale to yellowish, hind femora with a dark mark on anterior face
slightly beyond the middle; claws brownish, arolia bristle-like, translucent, erect
and converging slightly apically, protruding slightly forward between the claws.
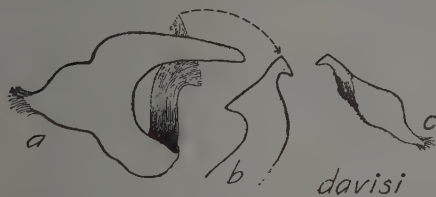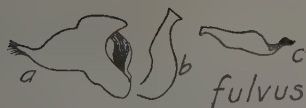
Fig. 18. *Deraeocoris fulvus*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: dark brownish to piceous, paler on sides of genital segment, shining, pale pubescent; genital claspers (fig. 18) distinctive of the species.

♀. Length 4.8 mm., width 2.22 mm., margin of embolium distinctly arcuated on apical half; head and disk of pronotum fulvous, collum black and shining, geminate mark on basal half of tylus blackish; scutellum pale to fulvous, somewhat fulvous on basal half of clavus; inner apical angles of corium and joining across anal area of membrane, brownish black to piceous, frequently a small spot at middle and base of corium fusco-brownish; cuneus yellowish translucent, more translucent at the lateral margin; ventral parts rather uniformly yellowish brown, infuscated along the vagina exterior; antennae pale to yellowish, segment II, 1.25 mm., slender, slightly thicker at apex, pale pubescent, length of exserted hairs slightly greater than thickness of segment.

Holotype: ♂ August 4, Williams, Arizona (H. H. Knight); Cornell University collection. *Allotype*: taken with the type. *Paratypes*: 2♂ 14♀, taken with the types on white oak *(Quercus sp.)*. ARIZONA,—2♀ Aug. 3, Grand View, Grand Canyon; ♀ Aug. 4, Prescott; ♂ 4♀ July 26, Mt. Lemon, alt. 9,000 ft., Santa Catalina Mts. (H. H. Knight). 9♀ July 27, Huachuca Mts., alt. 9,000 ft. (H. G. Barber).

KEY TO THE SPECIES OF GROUP IV

1. Black, shining, scutellum red, head reddish . . . . . .
   . . . . *fulgidus* Van D. p. 149
   Sometimes black but scutellum not red; entirely pale, or grayish testaceous and marked with black 2

2. Membrane clear, dorsum pallid, usually marked with black on the calli, corium sometimes fuscous on the apical half; infuscation on scutellum forming along the median line . . . *schwarzii* Uhler p. 146
   Membrane infuscated or at least fumate, dorsum black, or pallid gray and marked with black; scutellum with infuscation forming on each side of the median line, black specimens may have the median line entirely black 3

3. Femora reddish or reddish brown, not distinctly banded on the apical half; scutellum reddish or reddish brown, becoming dark brown or blackish at each side of the median line; venter strongly reddish, varied with yellowish brown; dorsum with suffused brownish invading the paler parts; middle, base and apex of corium, and apex of embolium infuscated . . . . . . *bullatus* n. sp. p. 147
   Femora twice banded on the apical half with reddish or reddish brown; scutellum pale yellowish, blackish spot each side of the pale median line; venter piceous to black on the lower side, narrowly yellowish at base and latero-dorsal margin . . *convexulus* n. sp. p. 148

Deraeocoris schwarzii (Uhler)

1893 *Camptobrochis schwarzii* Uhler, Proc. Ent. Soc. Wash., ii, p. 375.
1909 *Camptobrochis schwarzii* Reuter, Acta Soc. Sci. Fenn., xxxvi, No. 2, p. 58.
1917 *Camptobrochys (Mycterocoris) schwarzii* Van Duzee, Cat. Hemip., p. 355.

Ovate, convex, pale, the head, calli, and corium marked with blackish, the dark color on scutellum forming along the median line.

♂. Length 4.5 mm. *Head*: width 1.03 mm., vertex .52 mm., length .54 mm.; front convex, carina not apparent but vertex is separated by a groove from the black and broadly exposed collum, tylus prominent; pale, spot each side of vertex, transverse marks each side of front and terminating above in a pair of large spots just in front of vertex, for a short space above base of antenna next to inner margin of eye, geminate mark on tylus with spot at base and transversely at apex, dorsal and apical margins of lorae, small spot on genae and juga, blackish. *Rostrum,* length 1.71 mm., scarcely attaining posterior margins of middle coxae, pale to brownish, becoming piceous at apex.

Antennae: segment I, length .37 mm., pale, becoming blackish on the ventral side; II, 1.14 mm., gradually thickened from base toward apex, not attaining the thickness of segment I, pale pubescent, length of exserted hairs exceeding thickness of segment, pale to brownish, becoming fuscous toward apex; IV, missing.

Pronotum: length 1.17 mm., width at base 1.97 mm., anterior angles 1 mm.; collar .72 mm., pale, opaque; disk convex, coarsely, rather irregularly and closely black punctate, lateral margins slenderly carinate, nearly straight, anterior angles rather broad but rounded; calli very slightly convex, black around margins and with marks upon the disk of each, a black arc projecting forward from the latero-anterior angles and with pale invading the disk each side of it; pale to ivory-white, somewhat shining; coxal cleft somewhat darkened above; xyphus nearly flat, margins carinate bordering the coxal cavity, pale. *Scutellum* convex and smooth, pale, becoming brownish along the median line; mesoscutum slightly exposed, brownish black. *Sternum* and pleura pale to dark brownish, episterna becoming blackish first; ostiolar peritreme pale, dorsal margin somewhat invaded by blackish.

Hemelytra: width 2.39 mm., convex, embolar margin slightly arcuate; black punctate but more finely than on pronotal disk, pale but not translucent, spot at middle and somewhat at apex of corium. piceous. *Cuneus* pale, opaque, finely black punctate, spot on inner margin at apex fuscous. *Membrane* clear, veins pale fusco-brownish, sometimes slightly invading and staining the membrane each side.

schwarzii Uhl.

Fig. 19. *Deraeocoris schwarzii*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Legs: pale, coxae with a dark brownish to blackish spot at base; femora biannulate with brownish black on apical half, sometimes with fuscous spots on the basal half; tibiae biannulate with blackish on the basal half; tarsi fuscous at apex, claws brownish.

Venter: dark brownish to piceous, shining, the pale color persisting lat-

erally and near base, a large somewhat rounded piceous spot beneath the spiracle on each side of the first four or five segments but pale just beneath the spots, pale pubescent; genital claspers (fig. 19) distinctive of the species.

♀. Length 4.9 mm., width 2.45 mm., more robust than the male and with the dark marks more reduced; scutellum may be entirely pale or with only a brown streak along the median line, infuscations of corium absent; geminate mark on tylus, anterior margin of lorae, collum, and marks about the margins of calli, blackish; segment II, length 1.17 mm., slender, enlarged toward apex, length of exserted hairs nearly equaling twice the thickness of segment, pale, dark brownish at apex; black markings on the legs usually much reduced.

Lectotype: ♂ June 22, 1891, American Fork, Utah (E. A. Schwarz); Cat. No. 24171 U. S. N. M. *Plesiotype*; ♂, cotype by Uhler; author's collection. *Specimens examined*: 2♂ 3♀ June 22, ♀ June 24, American Fork, Utah (E. A. Schwarz); ♀ July 8, 9, 1882. Yakima river, "Opp. Ellenberg," Washington Territory (Hagen); all cotypes by Uhler. ♂ "Colo. 2020" which has the median line on front obscured by piceous. The specimen taken by Dr. Hagen near the Yakima river is more heavily marked with black than is the case with the females from the type locality.

This species was collected by Mr. Schwarz on desert vegetation near American Fork, and, as the color and other characteristics indicate, it is a form to be expected only in the arid regions of the United States.

Deraeocoris bullatus new species

More convex and darker colored than *schwarzii*, scutellum red, becoming blackish each side of median line, membrane infuscated on the apical half.

♂. Length 4.7 mm. *Head*: 1.03 mm., vertex .51 mm., length .57 mm.; carina slight but apparent, front broadly convex, collum broadly exposed and dark yellowish like the rest of the head; geminate mark and transversely at tip of tylus blackish, juga frequently with reddish. *Rostrum,* length 1.91 mm., reaching upon the hind coxae, dark brownish to piceous.

Antennae: segment I, length .37 mm., dark fusco-brownish; II, 1.2 mm., slender on the basal half, gradually enlarged on the apical half and nearly attaining the thickness of segment I, pale pubescent, exserted hairs slightly exceeding greatest thickness of segment, piceous to black; III, .45 mm.; IV, .34 mm.; last two segments slender, blackish.

Pronotum: length 1.22 mm., width at base 2.08 mm., anterior angles 1.05 mm.; collar .74 mm., yellowish brown, opaque; disk convex, lateral margins distinctly carinate, nearly straight, the anterior angles broadly rounded; disk coarsely black punctate, punctures arranged irregularly in small groups, more sparsely placed across the middle; calli smooth, slightly convex, confluent, delimited behind by coarse punctures, black, the black color projecting forward at the latero-anterior angles; pale to sordid ivory-white, posterior lobes of disk

becoming suffused with piceous, the median line more pale; propleura pale brownish, opaque, paler at margins, more finely punctate than disk; xyphus nearly flat, yellowish to brownish. *Scutellum* convex, smooth, dark reddish to brownish, median line paler, becoming blackish each side at base; mesoscutum scarcely exposed, reddish brown. *Sternum* and pleura brown, opaque; ostiolar peritreme pale, becoming brownish above.

Hemelytra: width 2.51 mm., convex, embolar margin arcuate; black punctate but more finely than on pronotal disk, pale, becoming stained with brownish and fuscous; slender edge of embolium but broadly at apex, apex of corium and spot at middle, piceous. *Cuneus* pale but not translucent, punctures, apical one-third, and narrowly at base, black. *Membrane* transversely pale across middle, brownish to fuscous on apical one-third, brachium and narrowly each side dark fuscous.

Legs: coxae pale, becoming reddish brown on anterior face; femora reddish brown, more translucent basally; tibiae fusco-brownish to blackish, biannulate with pale, frequently a third pale indication at knee; tarsi brownish to blackish, claws brown, distinctly cleft; arolia erect, bristle-like, parallel or slightly divergent apically.
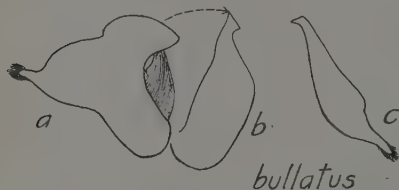
Fig. 20. *Deraeocoris bullatus,* male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: pale to reddish or reddish brown, becoming piceous on base of genital segment, pale pubescent; genital claspers (fig. 20) distinctive of the species.

♀. Length 4.5 mm., width 2.65 mm., slightly more robust but very similar in color to the male; segment II, length 1.22 mm., slender, slightly enlarged on the apical one-fourth, pale pubescent, exserted hairs equaling greatest thickness of segment, piceous, a dark brownish band just beyond middle.

Holotype: ♂ August 3, Grand View, Grand Canyon, Arizona (H. H. Knight); Cornell University collection. *Allotype*: taken with the type. *Paratypes*: ♂ 4♀ taken with the types on the cliff rose, *Cowania mexicana,* while the shrub was in flower. ♂ 2♀ June 18, Ashfork, Arizona (Barber & Schwarz).

This species doubtless breeds on the cliff rose and was not merely attracted by the flowers as may be the case with some insects. *D. manitou intermedius* bears a close resemblance to *bullatus* but the color of the legs as well as the structure of the claws makes their separation simple.

Deraeocoris convexulus new species

Very similar to *bullatus,* paler above and without red on scutellum and venter, hind femora twice banded on the apical half with reddish brown; left

genital clasper with the dorsal horn longer and the internal arm differently shaped from that of *bullatus.*

♂. Length 4.6 mm. *Head*: width 1.05 mm., vertex .54 mm., length .57 mm.; base of vertex raised into a slight carina, separated by a groove from the arched and broadly exposed collum; pale to yellowish, geminate mark on basal half and slenderly at apex of tylus blackish. *Rostrum*, length 1.88 mm., attaining posterior margins of middle coxae, brownish, becoming piceous on the apical half.

Antennae: segment I, length .38 mm., brownish, darker at apex; II, 1.25 mm., tapering gradually thicker from base toward apex, attaining the thickness of segment I, pale to dusky pubescent, exserted hairs about equaling greatest thickness of segment; III, .51 mm.; IV, .37 mm.; last two segments slender, blackish.

Pronotum: length 1.11 mm., width at base 2.04 mm., anterior angles 1.03 mm., collar .77 mm.; structurally and in color very similar to *bullatus,* the disk and calli slightly more flattened. *Scutellum* convex and smooth, pale, brownish black or piceous each side of median line but scarcely separating the pale at basal angles from that at apex. *Sternum* and pleura yellowish brown, opaque; ostiolar peritreme pale yellowish.

Hemelytra: width 2.57 mm., very similar to *bullatus* but more coarsely punctate; pale, small spot at base, transversely at apex and connected with spot at middle of corium, invading the embolium at apex, blackish. *Cuneus* as in *bullatus. Membrane* nearly as in *bullatus* but paler on the apical half, more nearly fumate.

Legs: pale to yellowish; femora biannulate on the apical half with reddish brown; tibiae triannulate with brownish black and with a spot on the knee; tarsi dark brownish, blackish at apex, claws brownish.
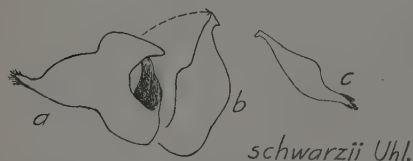

Fig. 21. *Deraeocoris convexulus,* male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: dark brownish to piceous, paler at the lateral margins and at base, shining, pale pubescent; genital claspers (fig. 21) distinctive of the species.

♀. Length 5.5 mm., width 2.9 mm., very similar to the male but more robust; antennae very similar to those of the female *bullatus.*

Holotype: ♂ May, Los Angeles County, California (Heidemann coll.); Cornell University collection. *Allotype*: same data as the type.

Deraeocoris fulgidus (Van Duzee)

1914 *Camptobrochis fulgidus* Van Duzee, Trans. San Diego Soc. Nat. Hist., ii, p. 21.

1917 *Camptobrochys (Mycterocoris) fulgidus* Van Duzee, Cat. Hemip., p. 355.

Length 5-6 mm. Ovate, convex, shining black, scutellum red, head rufotestaceous.

♂. Length 5 mm. *Head*: width 1.12 mm., vertex .57 mm., length .6 mm.;

carina slight but apparent, front broadly convex, collum broadly exposed; rufo-testaceous, tip of tylus and the bucculae becoming black. *Rostrum,* length 2.08 mm., nearly attaining posterior margins of middle coxae, piceous.

Antennae: segment I, length .43 mm.; II, 1.42 mm., slender at base and gradually enlarged to thicker at apex, the greatest thickness just equaling that of segment I, dusky pubescent, exserted hairs equal to one and one-half times the thickness of segment I; III, .52 mm.; IV, .43 mm.; all the segments black.

Pronotum: length 1.4 mm., width at base 2.31 mm., anterior angles 1.12 mm.; collar .85 mm., dark brownish, opaque; lateral margins carinate, nearly straight, anterior angles broadly rounded and slightly reflexed; closely and coarsely punctate, calli convex, confluent, delimited posteriorly by coarse punctures; basal margin of disk sometimes slenderly pale; propleura black, opaque, finely punctate; xyphus nearly flat, dark brownish to black. *Scutellum* rufo-testaceous to bright red, convex, smooth and shining. *Sternum* and pleura dark brownish or black, opaque; ostiolar peritreme pale, becoming blackish above and within the ostiole.

Hemelytra: width 2.9 mm., embolar margin strongly arcuated on the apical half, embolium broad; more closely punctate than on the pronotal disk. *Cuneus* nearly triangular, strongly deflexed, sometimes palely translucent near inner angles. *Membrane* brownish black, paler spot bordering tip of cuneus.

Fig. 22. *Deraeocoris fulgidus,* male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: black, shining, pale pubescent; genital claspers (fig. 22) distinctive of the species, in form nearest to *bullatus*.

♀. Length 5.1 mm., width 2.82 mm., very similar to the male in form and coloration; segment II, length 1.34 mm., slender, thickened on the apical one-fourth, scarcely attaining the thickness of segment I, dusky pubescent, exserted hairs equal to twice the thickness of segment.

Plesiotypes: ♂ June 6, ♀ May 4, San Diego County, California (E. P. Van Duzee), paratypes; author's collection. *Specimens examined*: CALIFORNIA,—♀ March 29, 1♂ 1♀ May 4, San Diego County, *paratypes* (E. P. Van Duzee). ♀ June 18, Hullville, Lake County (F. E. Blaisdell). ♀, McCloud, Siskiyou County (E. P. Van Duzee). COLORADO,—♂ June 28, Fort Collins (E. P. Van Duzee).

Mr. Van Duzee states that the species lives on Ceonothus.

KEY TO THE SPECIES OF GROUP V

In form of the claws this group shows a close relationship with the species of group II but the impunctate scutellum, genital claspers, general body structure and hairy vestiture of some of the species all point to a closer relationship with the species in groups IV and VI.

1. Dorsum heavily pubescent or hairy, at least with long hairs at anterior
    angles of the pronotum 12
   Dorsum practically glabrous, at most only sparsely and finely pubescent
    (not rubbed specimens), rarely with a few hairs at anterior angles
    of pronotum . . . . , ... 2
2. Form broad oval, strongly convex (width greater than or equal to at
    least one-half the length of the insect) 3
   Form elongate (width not equal to one-half the length) . . . 4
3. Tibiae triannulate with fuscous; disk of pronotum more or less pale,
    becoming blackish on the basal half and sides; scutellum with black spot
    each side of the pale median line, but confluent at base; apex of corium
    and embolium broadly blackish, usually joined by large spot on middle
    of corium, apical one-third of cuneus black . . . . .
    . . . . *manitou* Van D. p. 153
   Tibiae triannulate with fuscous; disk of pronotum black, narrowly mar-
    gined with pale; scutellum black, basal angles and tip pale; hemelytra
    black, basal half of embolium, central portion of clavus, basal half of
    cuneus, small spot near base of corium, and narrowly bordering basal
    half of cubitus, irregularly pale, the punctures black . . .
    . . . . *manitou intermedius* n. var. p. 154
   Tibiae pale, slightly darker at tips and indistinctly so at middle; dorsum
    entirely black; head pale, genae, bucculae, margins of lorae, and gem-
    inate mark on the tylus, piceous to black . . . .
    . . . . *manitou atratus* n. var. p. 155
4. Membrane with the apical half heavily infuscated; pronotum and
    hemelytra usually blackish, in tenerel or pale specimens more or less
    translucent but darkened with fuscous or brownish . . . 7
   Membrane with the apical half only slightly infuscated, more nearly
    fumate or brownish; dorsum more pallid, yellowish or reddish than
    blackish, calli ferruginous or heavily lined with black around the mar-
    gins and with one or two pale streaks on the disk of each callus . 5
5. Membrane clear, a fumate cloud on the apical half; calli heavily mar-
    gined with brownish or black, forming a recurved hook at the latero-
    posterior margins; punctures infuscated, dorsum lurid testaceous with
    three darker areas on each hemelytron . . . . . .
    . . . . *barberi hesperus* n. subsp. p. 159
   Membrane uniformly fumate or brownish; calli without a blackish re-
    curved hook at the latero-posterior margins; punctures mostly pel-
    lucid, dorsum pallid to pale yellowish or reddish brown to reddish . 6
6. Calli and pronotum reddish brown to ferruginous; hemelytra yellow-
    ish translucid, immaculate; cuneus reddish translucent; scutellum
    pale . . . . *rubroclarus* n. sp. p. 156
   Calli margined or lined with black; corium pallid to yellowish, tinged
    with brown ochre and reddish, opaque except for pellucid punctures;
    cuneus yellowish, opaque, the apex blackish; scutellum vittate . .
    . . . . *navajo* n. sp. p. 155
7. (4) Antennae (♀) with prominent exserted hairs on segment II, in
    length equal to three times the thickness of segment at middle; (♂)
    segment II as thick at the middle as on the apical half, length of ex-

serted hairs equal to one and one-half times the thickness of the seg-
ment . . . . *laricicola* n. sp. p. 164
Antennae (♀) with exserted hairs, in length scarcely equal to twice the
thickness of the segment where they occur: (♂) segment II slender
on the basal half, distinctly thicker on the apical half than at middle,
or if not, then the length of exserted hairs not greater than the thick-
ness of the segment.   8

8. Calli margined or lined with black, rarely entirely black, ivory-white
just before and extending inward from the anterior angles in one or
two curved lines upon disk of each callus; (♂) segment II of an-
tennae nearly as thick at middle as on the apical half, length of ex-
serted hairs scarcely as great as the thickness of the segment   .
. . . . *pinicola* n. sp. p. 162
Calli solid black; segment II very similar in both sexes, slender on the
basal half and gradually becoming thicker toward the apex, exserted
hairs about equal to thickness of the segment   9

9. Tibiae distinctly triannulate with pale; a small subovate form, length
5-5.5 mm. . . . . *mutatus* n. sp. p. 161
Tibiae uniformly dark, or pale on the apical half, sometimes with a
pale indication just below knee and obscurely banded with pale on the
apical half but never distinctly triannulate; larger forms, length close
to 6 mm.   10

10. Scutellum uniformly brownish; hind tibiae broadly pale on apical half
but without a pale indication below knee . . . . .
. . . . *appalachianus* n. sp. p. 160
Scutellum blackish, marked with pale at least on basal angles and at
apex; hind tibiae dark, or an obscure pale band on apical half and
usually a pale indication just below knee   11

11. Femora paler on the basal half, hind tibiae usually with an obscure
pale annulus on the apical half and a pale indication just below knee
. . . . *barberi* n. sp. p. 157
Femora and tibiae uniformly dark brownish black . . . .
. . . . *barberi lignipes* n. var. p. 159

12. (1) Legs uniformly dark sepia brown or blackish, hind tibiae fre-
quently with a pale annulus on the apical half   15
Legs not uniformly sepia black, femora more or less pale or the tibiae
biannulate with paler   13

13. Legs and general body coloration fusco-grayish to blackish, never red-
dish brown; hind femora pale on the basal half, two or three linear
series of dark spots visible, apical half dark fuscous to blackish but
divided by a narrow pale annulation; tibiae biannulate with pale   .
. . . . *kennicotti* n. sp. p. 166
Legs and usually the body coloration dark reddish brown to blackish;
hind femora obscured on the basal half, more or less reddish brown,
pale annulation usually apparent on the apical half; tibiae dark red-
dish to brownish, either bi- or triannulate with pale   14

14. Hemelytra grayish testaceous to brownish, distinctly darker or even
piceous on the apical half of the corium; hind tibiae with a distinct

pale annulus on the apical half, two narrow and poorly defined pale
annuli on the basal half, the pale band at middle of basal half usually
incomplete on the dorsal side   .   .   *fulvescens* Reuter p. 167
Hemelytra uniformly reddish brown, not darker on the apical half of
the corium than on the embolium; hind tibiae triannulate with pale
.   .   .   . *pilosus* n. sp. p. 169

15. Pronotum, hemelytra and legs uniformly dark sepia brown or blackish,
the semitranslucent areas stained with brownish; hind tibiae usually
distinctly annulated with pale on the apical half   .   .   .   .
.   .   .   .   .   *nigritulus* n. n. (=|| *nigritus* Reut.) p. 170
Pronotum usually fusco-grayish or black; hemelytra fuscous to black,
becoming paler in certain areas but not stained with brownish; legs
brownish black, hind tibiae sometimes indistinctly annulated with paler
on the apical half; front coxae, xyphus, lower margins of propleura,
ostiolar area, gula, sides of tylus, juga and arcuated streak just
above on each side of front, pale   .   .   *albigulus* n. sp. p. 171

Deraeocoris manitou (Van Duzee)

1904 †*Mycterocoris cerachates* Uhler, Proc. U. S. Natl. Mus., xxvii, p. 358.
1920 *Camptobrochys manitou* Van Duzee, Proc. Calif. Acad. Sci., ser. 4, ix,
p. 355.

Length 4.5-5 mm. Ovate, convex, dorsum glabrous, coarsely punctate;
closely related to *bullatus* and *convexulus* but differs in the type of claws; more
ovate and robust than *fenestratus;* pale to testaceous and maculated with
piceous, callosities and punctures black.

♂. Length 4.5 mm. *Head*: width 1.03 mm., vertex .54 mm., length .71
mm.; front moderately convex, polished, carina feebly developed; collum ex-
posed, black; yellowish and marked with brown and black, front each side of
median line transversely marked with six or seven fine brownish to blackish
lines; above base of antenna, bordering the front margin of eyes and projecting
on vertex, brownish to piceous; slender pair of longitudinal lines on tylus,
base of genae, dorsal margins of lorae and bucculae, brownish to piceous,
frequently reddish on juga. *Rostrum,* length 1.85 mm., reaching to near hind
margins of middle coxae, yellowish brown, basal segment darker, the apical
segment piceous.

Antennae: segment I, length .35 mm., yellowish, a brownish line on the
dorsal side; II, length 1.14 mm., yellowish to brownish, apical one-fifth in-
fuscated, basal one-third dark brownish on the dorsal side; III, .45 mm.,
blackish; IV, .40 mm., blackish; finely pale pubescent, length of hairs on seg-
ment II equal to little more than the thickness of segment.

Pronotum: length 1.2 mm., width at base 2.05 mm.; anterior angles 1.05
mm., strongly rounded; collar .71 mm., brownish; disk deeply, irregularly, some-
times confluent but not densely punctate, strongly convex, lateral margins slen-
derly carinate, nearly straight, anterior and basal angles broadly rounded; pale
yellowish, discal area each side of middle clouded with piceous; calli black,
practically flat, joined at the anterior angles by a piceous arc; very finely and
sparsely pubescent at anterior angles; propleura yellowish, becoming reddish

anteriorly, xyphus reddish; margin of coxal cavity anterior to coxal cleft very prominent, flaring, narrow margin white. *Scutellum* impunctate, convex and polished, obscurely transversely wrinkled; whitish, piceous medially at base and extending to cover lateral areas of disk; mesoscutum brownish to piceous, paler at lateral angles. *Sternum* and pleura reddish; ostiolar peritreme white.

Hemelytra: width 2.68 mm., strongly convex, embolium arcuate from base to apex, cuneus and membrane strongly deflexed; coarsely and irregularly punctate, punctures black, surrounded by piceous and frequently confluent; clavus largely pale, piceous at apex and along margins; corium broadly piceous at apex and invading embolium, narrowly piceous at base, a larger patch at middle which is rather broadly joined with the piceous distal area; embolium largely pale, apex, slightly at middle, bordering the marginal vein and the extreme lateral edge, piceous. *Cuneus* pale, the apical one-third piceous, punctures infuscated. *Membrane* fuscous, a paler band bordering apices of areoles, joining at middle and continuing medially between the large areoles, veins piceous.

Legs: femora uniformly piceous, pale at the apices; tibiae pale, triannulate with fuscous or piceous, an oblique band at middle, less distinctly near base and rather broadly but paler at apex; tarsi pale fuscous, slightly darker at apices; clothed with fine inconspicuous pale pubescence.

Venter: reddish to piceous, polished, finely pale pubescent; genital claspers (fig. 23) distinctive of the species.

♀. Length 5.4 mm., width 3 mm.; larger and more robust than the male but very similar in coloration.

manitou VanD.

Fig. 23. *Deraeocoris manitou*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Plesiotype: ♂ July 19, Manitou, Colorado (E. P. Van Duzee); *holotype*, (No. 713) collection of California Academy of Sciences. *Paratypes examined*: COLORADO,—2♀ July 25, Manitou (E. P. Van Duzee); 3♀ July 17, ♀ Aug. 7, Colorado Springs; ♀ July 25, Rifle. NEW MEXICO,—♀ Aug. 1-15, Jemez Springs, alt. 6,400 ft. (Woodgate). *Specimens examined*: ARIZONA,—3♀ June 18, Ashfork (H. S. Barber). NEW MEXICO,—♀ Aug. 10, ♀ Aug. 16, Las Vegas (Barber & Schwarz).

The last two specimens mentioned represent the material which Uhler (1904) had before him when describing the new genus *Mycterocoris* and thus the genus was founded on a misidentification of his own species, *Deraeocoris cerachates*.

Deraeocoris manitou intermedius new variety

Structurally not differing from the typical *manitou* but having a different color aspect; disk of pronotum black, slenderly margined with pale, some-

times slightly paler behind the calli; scutellum black, basal angles and apex pale or ivory-white; hemelytra black, basal half of embolium, central portion of clavus, basal half of cuneus, small spot near base of corium, and narrowly bordering basal half of cubitus, irregularly pale between the black punctures; tibiae triannulate with fuscous.

Holotype: ♂ Aug. 1-15, Jemez Springs, New Mexico (J. Woodgate); author's collection. *Allotype*: same data as the type. *Paratypes*: ♂ July 7, ♀ July 21, ♀ Aug. 1-15, Jemez Springs, New Mexico (J. Woodgate).

Deraeocoris manitou atratus new variety

Apparently not differing structurally from the typical *manitou;* dorsum entirely black; head pale, genae, bucculae, margins of lorae, and geminate mark on tylus, piceous to black; tibiae pale, slightly darker at tips and indistinctly so at middle.

Holotype: ♂ June 17, Jemez Springs, New Mexico (J. Woodgate); author's collection. *Allotype*: same data as the type. *Paratypes*: ♂♀ taken with the types. ARIZONA,—1♂ 1♀ June 17, 2♂ 2♀ June 18, ♀ June 28, Ashfork (H. S. Barber).

It is worthy of note that in this variety the legs are paler than the typical *manitou* while the dorsum has grown entirely black. The development in color seems to run thus: the blacker the dorsum the paler the legs.

Deraeocoris navajo new species

Dorsum pallid to yellowish, tinged with brown ochre and reddish, punctures chiefly pellucid, calli and vittate marks on scutellum blackish, membrane fumate.

♂. Length 5.6 mm. *Head*: width 1.2 mm., vertex .54 mm., length .63 mm.; facial angle less than a right angle, carina poorly defined, the brownish collum moderately exposed, an impressed brownish spot each side of vertex; pale to yellowish, rather indistinct reddish to brownish transverse marks each side of frontal median line; triangular mark at base and geminate mark on basal half of tylus, dorsal margin of lorae, above base of antenna and reaching inner margin of eye, blackish, a reddish spot beneath the rather large brown eyes. *Rostrum,* length 2.51 mm., nearly attaining the posterior margins of hind coxae, brownish to piceous, darker at apex.

Antennae: segment I, length .4 mm., yellowish, becoming infuscated at base and narrow apex; II, 1.63 mm., slender at base and gradually thickened toward apex, exceeding the thickness of segment I, pubescence infuscated, exserted hairs about equaling greatest thickness of segment, yellowish to brown, the apical half black; III, .63 mm.; IV, .44 mm.; last two segments black, finely pale pubescent.

Pronotum: length 1.35 mm., width at base 2.25 mm., anterior angles 1.05 mm.; collar .88 mm., prominent, yellowish and opaque; disk convex, punctures chiefly concolorous or pellucid, becoming infuscated at basal angles, lateral margins distinct, slightly sinuate, anterior angles narrowed but distinct; calli slightly convex, irregularly delimited behind by coarse punctures, separated at median line by a pair of punctures, black, a blackish arc extending forward from the antero-lateral angles; propleura more finely punctate than disk, pale to yellowish, a reddish brown spot at top of coxal cleft; xyphus practically flat, longly but sparsely pale pubescent. *Scutellum* convex, shining, slightly wrinkled on disk, yellowish, a brownish black vitta each side of median line on the apical half; mesoscutum moderately exposed, yellowish brown. *Sternum* and pleura yellowish to brownish, opaque, meta-episterna tinged with reddish; ostiolar peritreme pale, becoming yellowish about the ostiole.

Hemelytra: width 2.77 mm., embolar margin sinuate; pale to yellowish, punctures chiefly pellucid, spot at base and middle of corium, transversely across tip of embolium, corium and clavus, stained with brown ochre and reddish. *Cuneus* pale to yellowish, chiefly opaque, punctures mostly infuscated, apex brownish black, slightly reddish at base. *Membrane* fumate, brachium distinctly reddish, a small fuscous mark lying against the brachium just outside apex of the larger areole.

Legs: pale to yellowish brown, each coxa with a pair of shining fuscous spots at base; femora indistinctly marked with reddish before apices; tibiae triannulate with reddish brown or fuscous, also a spot on the knee; tarsi brownish, infuscated at apices, claws not cleft at base, arolia slender, erect, bristle-like, translucent, nearly parallel or only slightly converging at apices.

Fig. 24. *Deraeocoris navajo*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: yellowish to reddish, two basal segments more broadly reddish, an impressed, polished piceous spot on each segment beneath the spiracle and separated from it by a space equal to diameter of spot; genital segment piceous, polished, a large yellowish spot each side near apex; genital claspers (fig. 24) distinctive of the species.

Holotype: ♂ August 3, Grand View, Grand Canyon, Arizona (H. H. Knight); Cornell University collection.

This very distinct and interesting species is represented only by the type specimen which was swept from the cliff rose *(Cowania mexicana)*. The failure to secure additional specimens indicates that its presence on that plant may have been accidental.

Deraeocoris rubroclarus new species

Elongate, calli and pronotum reddish brown to ferruginous, scutellum pale; hemelytra yellowish translucid, immaculate, cuneus reddish translucent.

♀. Length 6.3 mm. *Head*: width 1.14 mm., vertex .55 mm., length .71 mm.; tylus more prominent at base than in *navajo*, facial angle a right angle, eye sloping slightly forward, carina obsolete, separated from the broadly exposed collum by a groove, front broadly convex, shining; yellowish red, geminate mark on tylus, spot on juga, spot on genae, and above base of antenna, bright red. *Rostrum*, length 2.31 mm., attaining the posterior margins of the middle coxae, brownish translucent, apex piceous.

Antennae: segment I, length .54 mm., yellowish translucent to brownish; II, 1.77 mm., slender, slightly enlarged on the apical one-fourth, not attaining the thickness of segment I, sparsely pale pubescent, length of exserted hairs about equal to greatest thickness of segment, yellowish, blackish on the thickened apex; III, .71 mm.; IV, .57 mm.; last two segments blackish.

Pronotum: length 1.51 mm., width at base 2.39 mm., anterior angles 1.03 mm., collar .83 mm.; rather finely and closely punctate, punctures concolorous, lateral margins distinct but ecarinate, nearly straight, anterior angles narrowed but distinct, lateral margins of disk sparsely set with pubescent hairs; calli convex, ferruginous, shining, usually slightly darker than the disk; propleura finely punctate, yellowish to brown; xyphus slightly convex anteriorly, depressed posteriorly. *Scutellum* convex, smooth and shining, pale or white, sometimes with a tinge of reddish; mesoscutum slightly exposed, brownish. *Sternum* and pleura yellowish to brownish or reddish, opaque; ostiolar peritreme white.

Hemelytra: width 2.9 mm., embolar margin slightly sinuate, moderately convex, rather closely punctate, punctures concolorous; yellowish translucid, marginal vein at tip of embolium and the inner angles of corium with coagulated red. *Cuneus* reddish translucent, darker red apically, punctures apparent but concolorous. *Membrane* uniformly stained with pale brownish, slightly paler at tip of cuneus, brachium somewhat reddish.

Legs: yellowish with coagulated reddish, sometimes turning brownish; femora obscurely biannulated with reddish on apical half; tibiae rather obscurely triannulate with reddish or brownish, darker on the apical band; tarsi brownish to fuscous, darker at apices, claws and arolia as in *navajo*.

Venter: brownish to bright red, slightly darker on the sides, yellowish pubescent.

Holotype: ♀ August 12, Portland, Oregon (A. A. Nichol); author's collection. *Paratypes*: ♀ Aug. 18, Sannich District, British Columbia (W. Downes). ♀, "W. T." [Washington Territory] (Uhler collection).

Data on the food habits are not available but judging by the habits of other species in the group, *rubroclarus* is most likely to be found by beating coniferous trees in the Vancouveran faunal area.

Deraeocoris barberi new species

Dark brownish to piceous, calli solid black, usually slightly larger than *pinicola;* antennae very similar in both sexes, exserted hairs equal to thickness of the segment.

♂. Length 6.1 mm. *Head*: width 1.2 mm., vertex .54 mm., length .65 mm.; facial angle scarcely equal to a right angle, front broadly convex, carina obsolete, vertex separated by a groove from the black and broadly exposed collum; pale testaceous, front rather broadly, base of tylus, above base of antenna and extending along front margin of eye where it terminates in a spot on vertex, geminate mark on tylus which may be fused in darkest specimens, spot on genae, dorsal margins of bucculae and lorae, more or less on juga and tip of tylus, blackish. *Rostrum*, length 2.62 mm., nearly attaining posterior margins of the hind coxae, dark brownish to piceous.

Antennae: segment I, length .43 mm.; II, 1.51 mm., gradually thickened from base toward apex, almost equaling the thickness of segment I, pale pubescent, length of exserted hairs just equaling thickness of segment; III, .54 mm.; IV, .47 mm.; fusco-brownish to blackish.

Pronotum: length 1.45 mm., width at base 2.31 mm., anterior angles 1.14 mm., collar .81 mm.; moderately convex, coarsely and rather closely punctate, lateral margins slenderly carinate, anterior angles slightly rounded but distinct; calli convex, confluent, black and shining, delimited behind by coarse punctures, a black arc extending forward from the antero-lateral angles to front margin of disk; punctures black, posterior lobes of disk largely fusco-brownish, paler near lateral margins and at anterior angles; propleura more finely punctate, brownish black, paler around the margins; xyphus slightly convex anteriorly, depressed posteriorly, testaceous to fuscous. *Scutellum* moderately convex, smooth and shining, brownish black, basal angles, apex, and median line pale or ivory-white. *Sternum* and pleura brownish black, opaque, a spot at dorsal margin of meso- and one on meta-episterna shining; ostiolar peritreme white, becoming infuscated dorsally.

Hemelytra: width 2.74 mm., embolar margin slightly sinuate, moderately convex, closely and rather coarsely black punctate; fusco-brownish to piceous, embolium paler between the punctures, apical half of corium piceous, becoming more nearly black at middle, extreme apical margin of corium more or less translucent. *Cuneus* fusco-brownish, more translucent on basal half and blackish at apex, punctures black. *Membrane* pale, fusco-brownish on the apical half and produced basally at middle, veins dark fusco-brownish, the areoles darkened apically, a blackish mark lying against the brachium just outside at apex of the larger areole.

Legs: fusco-brownish, basal half of femora paler but with dark points, hind femora darker on apical half but broken by an obscure and interrupted pale mark before apex; tibiae dark fusco-brownish, frequently paler at middle of the apical half, sometimes with a pale mark just below the knee but never distinctly triannulate; tarsi dark brownish to blackish, claws brownish translucent; arolia slender, bristle-like, translucent, erect and protruding forward in front of the claws, nearly parallel but diverging somewhat apically.
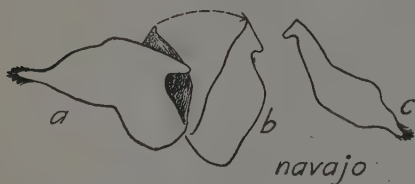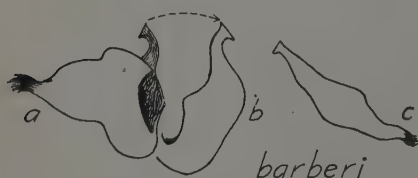

Fig. 25. *Deraeocoris barberi*, male genital claspers. a, left claspers, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: brownish black to piceous, pale pubescent; genital claspers (fig. 25) distinctive of the species.

♀. Length 6.6 mm., width 3.1 mm.; very similar to the male in form and coloration; segment II, length 1.6 mm., slightly more slender than in the male, gradually thickened on the apical half, length of exserted hairs slightly greater than thickness of segment.

Holotype: ♂ August, 1906, Glen Sioux County, Nebraska (H. G. Barber); author's collection. *Allotype*: taken with the type; collection of H. G. Barber. *Paratypes*: ♂ 12♀ taken with the types. ARIZONA,—July 3, Flagstaff (H. S. Barber). ♂ 2♀ July 17, Williams (Barber & Schwarz). COLORADO,—♂♀ July 21, Golden (W. J. Gerhard). ♀ July 23, Pine (C. A. Hill). MONTANA,—2♀ Sept. 11, Bear Paw Mountain (Uhler collection). NEW MEXICO,—♀ Aug. 13, Las Vegas (H. S. Barber).

This species is named in honor of Mr. H. G. Barber who is known for his excellent work on the Heteroptera and particularly the family Lygaeidae. Mr. Barber is not certain of the tree from which the specimens of this species were collected but thinks that it must have been pine.

Deraeocoris barberi lignipes new variety

Not differing structurally from the typical *barberi;* dorsum more uniformly stained with dark brownish; legs uniformly dark brownish black, shining.

Holotype: ♂ July 29, Huachuca Mountains, Arizona (H. G. Barber); author's collection.

Deraeocoris barberi hesperus new subspecies

Structurally very close to if not identical with the typical *barberi,* but differs at least in the general color aspect; calli outlined with piceous and forming a recurved hook at the latero-posterior margins, marked with pale or brown on the disk of each callus; basal half of femora pale, tibiae triannulate with pale, membrane clear, a fumate cloud on the apical half.

♂. Length 5.9 mm. *Head*: width 1.17 mm., vertex .54 mm., length .71 mm.; median line of front and an arc at each side touching the eye pale; broad arc composed of short transverse piceous bars each side of the pale median line and joining above, a piceous spot projecting from each eye upon the vertex. *Rostrum,* length 2.48 mm., reaching to near posterior margins of hind coxae, yellowish to brownish.

Antennae: similar to *barberi,* brownish to piceous, darker toward apex of segment II, segments III and IV blackish.

Pronotum: structurally very similar to *barberi;* testaceous to brownish, front margin and anterior angles largely pale; calli outlined with piceous, forming a recurved hook at the latero-posterior margins, disk irregularly marked with pale or brownish, a piceous line through the middle of each; anterior

angles with a thick piceous line leading to each callus. *Scutellum* piceous, the basal angles, median line and apex, pale. *Sternum* and pleura brownish to piceous; ostiolar peritreme white.

Hemelytra: width 2.65 mm.; testaceous to brownish, somewhat translucid; corium with whitish spot near base, a larger similar spot on the apical half but more or less divided by fusco-piceous; narrowly at base, between pale spots and more broadly at apex of corium, fusco-piceous. *Cuneus* testaceous, translucid, apex dark brownish to piceous, inner margin next to base of smaller areole pale. *Membrane* clear, fumate cloud on apical half, veins and slightly invading the membrane, dark brownish.

Legs: basal half of femora pale, apical half with two fusco-brownish or reddish brown annulations; tibiae triannulate with pale and with fusco-brownish; tarsi brownish to piceous.

Venter: brownish to piceous, shining; genital claspers are not appreciably different from the typical *barberi* (fig. 25).

Holotype: ♂ August 24, 1916, Summit, alt. 7,000 ft., Placer Co., California (W. M. Giffard); collection of California Academy of Sciences. *Allotype*: same data as the type. *Paratypes*: CALIFORNIA, —2♀, topotypic. ♀ July 24, Huntington Lake (E. P. Van Duzee). 1♂ 2♀ Aug.-Sept., Placer County.

Deraeocoris appalachianus new species

Closely related to *barberi,* general aspect more suggestive of a pale *nigritulus* but differs in the glabrous dorsum and short hairs on tibiae; scutellum uniformly brownish, less convex than in *barberi;* tibiae reddish brown, broadly pale on the apical half.

♀. Length 6.2 mm. *Head*: width 1.17 mm., vertex .57 mm., length .68 mm.; facial angle a right angle, outline of tylus more rounded and the head less pointed than in *barberi;* marked similarly to *barberi* but the black color replaced with brownish black. *Rostrum,* length 2.48 mm., attaining middle of the hind coxae, dark brownish, basal segment piceous.

Antennae: segment I, length .51 mm., fusco-brownish; II, 1.57 mm., slender, thickened on the apical one-fourth but not attaining the thickness of segment I, length of exserted hairs equal to twice thickness of segment at middle, fusco-brownish, darker at apex; III, .68 mm.; IV, .54 mm.; last two segments brownish to black.

Pronotum: length 1.34 mm., width at base 2.34 mm., anterior angles 1.14 mm., collar .83 mm.; disk more closely and uniformly punctured than in *barberi,* rather uniformly dark fusco-brownish, calli and anterior margin of disk brownish black; propleura dark brownish, paler at lower margins; xyphus nearly flat, testaceous, pale pubescent. *Scutellum* more flattened than in *barberi,* smooth and shining, minutely rugulose across the middle, uniformly dark brownish. *Sternum* and pleura dark brownish; ostiolar peritreme darkened with brownish.

Hemelytra: width 2.88 mm., embolar margin slightly more arcuate than in *barberi;* fusco-brownish, clavus and base of corium more yellowish and semi-translucent, embolium paler and semitranslucent, punctures brownish to fus-

cous. *Cuneus* dark brownish, slightly paler at middle, punctures dark brown. *Membrane* fusco-brownish, paler each side opposite tip of cuneus, membrane extending beyond tip of cuneus for a space about equal to length of cuneus.

Legs: fusco-brownish or reddish brown, tips of coxae and basal half of femora paler, apical half of femora without pale indications; tibiae dark brown or reddish brown, apical half broadly pale, hind tibiae slightly curved, length of longest hairs scarcely equal to thickness of segment; tarsi fusco-brownish, claws and arolia very similar to those of *barberi*.

Venter: dark brownish to piceous, shining, pale pubescent.

Holotype: ♀ May 21, (at light) Tryon, North Carolina (W. F. Fiske); author's collection.

This species is most closely allied to *barberi* and related forms, all of which are western in distribution. We may, therefore, regard *appalachianus* as another link in the list of known species which indicate a relationship between the fauna of the southern Appalachian region and the mountain faunas of the western United States.

Deraeocoris mutatus new species

In form and coloration very suggestive of a small specimen of *barberi* but more ovate; tibiae triannulate with pale, left genital clasper with a well-developed dorsal horn.

Length 5.3 mm. *Head*: width 1.12 mm., vertex .51 mm., length .56 mm.; similar to *barberi* but more broadly black, front and vertex solid black, leaving only the basal margin of head at each side of middle, and a slender lunate mark arising at base of tylus and curving up near front margin of eye, pale. *Rostrum*, length 2.31 mm., nearly attaining posterior margins of hind coxae, brownish to piceous.

Antennae: segment I, length .31 mm.; II, 1.2 mm., gradually enlarged from base toward apex, attaining the thickness of segment I, dusky pubescent, length of exserted hairs about equal to greatest thickness of segment; III, .48 mm.; IV, .43 mm.; all the segments brownish black.

Pronotum: length 1.2 mm., width at base 1.97 mm., anterior angles 1 mm., collar .77 mm.; disk moderately convex, lateral margins sinuate, slenderly carinate on the basal half, anterior angles narrowed; calli convex, black, a black mark from the antero-lateral angles lying in a depression adjoining anterior angles of disk; posterior half of disk brownish to piceous, the slender basal margin pale; propleura and xyphus nearly as in *barberi*. *Scutellum* moderately convex, smooth and shining, black, basal angles and apex pale to ivory-white, the median line not indicated. *Sternum* and pleura similar to those of *barberi*.

Hemelytra: width 2.48 mm., embolar margin slightly arcuate; paler than in *barberi*, apical half of corium darkened, more distinctly piceous on a spot at the middle. *Cuneus* comparatively large, length of outer margin greater than the distance from tip of cuneus to apex of membrane; black punctate, somewhat translucent, blackish at apex. *Membrane* infuscated as in *barberi* but in length more abbreviated.

Legs: dark fusco-brownish, trochanters and tips of coxae paler; femora obscurely biannulate with pale at the apices, the band somewhat removed from apex, is interrupted on the anterior face; tibiae triannulate with pale, the basal band just below knee narrow while the band on apical half is comparatively broad; tarsi dark brownish to blackish, claws yellowish translucent, structure of claws and arolia similar to those in *barberi*.
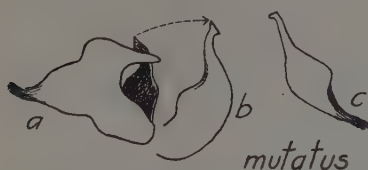
Fig. 26. *Deraeocoris mutatus*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: brownish black, shining, pale pubescent; genital claspers (fig. 26) distinctive of the species.

Holotype: ♂ August 22, Tallac, Eldorado County, California (W. M. Giffard); collection of California Academy of Sciences.

Deraeocoris pinicola new species

Closely related to *barberi* but differs in the antennae and genital claspers and usually is smaller in size; median line of front and just before the calli, pale to ivory-white, antero-lateral angles of calli invaded with pale; general coloration pale to grayish and darkened with blackish, not at all tinged with brownish.

♂. Length 5.7 mm. *Head*: width 1.08 mm., vertex .53 mm., length .57 mm.; carina obsolete, collum broadly exposed, black and shining, separated from the vertex by a groove; pale to ivory-white, front with a black arc each side of median line, broken into transverse bars in pale specimens; bordering front margin of eyes and terminating in a projection on vertex, base and apex of tylus with two connecting longitudinal lines, stripe from lower margin of eye across gena and upon the buccula, apically on lorae, and frequently a spot on juga, black, eyes dark brown. *Rostrum*, length 2.34 mm., reaching to near apices of hind coxae, piceous, paler at the joints.

Antennae: segment I, length .42 mm.; II, 1.51 mm., slender on basal one-fourth, practically cylindrical on the apical half and equal to segment I in thickness, dusky pubescent, length of exserted hairs about equaling thickness of segment; III, .6 mm.; IV, .5 mm.; all the segments black, shining.

Pronotum: length 1.34 mm., width at base 2.19 mm., anterior angles 1 mm.; collar .74 mm., fusco-grayish, opaque; disk moderately convex, coarsely black punctate but more closely and less deeply on the posterior half, lateral margins slenderly carinate, nearly straight, anterior angles rounded but distinct; calli convex, partially separated by a pair of punctures, black and shining but invariably invaded by pale at the latero-anterior angles where a black arc extends to front margin of disk, pale to ivory-white just before; posterior lobes of disk becoming darkened with piceous and black, slender basal margin pale; propleura black punctate, black and opaque surrounding the dorsal half of coxal cleft, margins more or less pale; xyphus nearly flat, infuscated on disk, anteriorly and the carinate lateral margins pale. *Scutellum* moderately convex, smooth and shining, black, basal angles, apex and median line more or less,

pale to ivory-white. *Sternum* and pleura black, opaque, a spot at dorsal margin of meso- and the meta-episterna shining; ostiolar peritreme white, becoming blackish above.

Hemelytra: width 2.68 mm., embolar margin moderately arcuate, slightly sinuate on the basal half; moderately convex, rather coarsely black punctate; pale to fuscous and black, more nearly black on apical half of corium and embolium, slenderly white along the cubitus near base. *Cuneus* moderately deflected, black, more or less pale on basal half, punctures black. *Membrane* rather heavily infuscated, a pale spot bordering tip of cuneus, basal half of areoles frequently somewhat paler, brachium and slightly invading the membrane more heavily infuscated.

Legs: black, tips of coxae and the trochanters paler; hind femora more or less pale on dorsal face of the basal half, an obscure pale mark on dorsal face just before apex; tibiae obscurely biannulate with pale; tarsi blackish, claws very slightly cleft (fig. 2, B) but should not be confused with the type which is deeply cleft near base; arolia slender, erect, bristle-like, translucent, nearly parallel but slightly converging at the very tips.

pinicola

Fig. 27. *Deraeocoris pinicola*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: black and shining, pale pubescent; genital claspers (fig. 27) distinctive of the species.

♀. Length 5.9 mm., width 2.9 mm., very similar to the male but paler in color; the black arc each side of front broken into transverse bars; segment II, length 1.6 mm., slender, thickened on the apical one-fourth, scarcely attaining the thickness of segment I, dusky pubescent, length of exserted hairs only slightly greater than thickness of segment, black as in the male; scutellum more broadly pale, the dark color frequently appearing as a black vitta from base each side of median line; femora more distinctly banded with pale before the apex, tibiae distinctly biannulate with pale; venter chiefly pale, a lateral row of spots, vagina exterior, and more or less on the ventral and anterior margins of segments, black.

Holotype: ♂ June 30, Ithaca, New York (H. H. Knight); author's collection. *Allotype*: same data as the type. *Paratypes*: CONNECTICUT,—♂ June 16, New Haven; ♀ July 22, Hartford (M. P. Zappe). ♀ July 11, New Haven (W. E. Britton). DISTRICT OF COLUMBIA,—♀ June 10, Rock Creek (O. Heidemann). MASSACHUSETTS,—3♀ July 18, Beach Bluff (H. M. Parshley). ♂ July 3, Danvers (C. W. Johnson). ♂ June 20, Natick (C. A. Frost). MINNESOTA,—3♀ Aug. 18, Elkhorn Creek, Carlton Co. (H. H. Knight), on *Pinus strobus*. NEW HAMPSHIRE,—1♂ 1♀ Mount Washington (Mrs. A. T. Slosson). ♀, Pike, "feeding on *Chermes*" [no authority]. NEW YORK,—♂ June 9, ♂ 2♀ June 13, 7♂ 18♀ June 14, 2♀

June 22, 2♂ 3♀ June 27, 2♂ 2♀ June 30, ♂ July 8, Ithaca; 6♂ 2♀ June 26, 12♂ 38♀ July 13, Ringwood near Ithaca (H. H. Knight), all taken on *Pinus strobus.* 1♂ 1♀ July 22, Conifer (H. Osborn).   ♂ June 18, 2♂ 5♀ July 8, Cranberry Lake; 2♀ Aug. 1-7, Wanakena (C. J. Drake). · 2♀ July 3, Wyandanch, Long Island (Wm. T. Davis). CANADA,—♀ "Milton, Can." [? Ontario] (Uhler collection).

The writer has found this species only on white pine, *Pinus stro-bus,* to which tree it appears to be restricted in its breeding habits. At Ithaca, on June 9, the fifth stage nymphs were found in numbers on two white pine trees. The nymphs were living among and were predaceous upon the pine bark aphid (*Chermes pinicorticis* Fitch), the predator being covered with a coat of white, wax-like, flocculent material, very similar to that which covered the aphids. On June 13, 1914, the adults were enferging rapidly and the next day most of them were out but many still in a tenerel condition. Most of the adults disappear before the last week in July, the females probably depositing their eggs in the terminal growth, there to spend the winter and hatch the following May.

Deraeocoris laricicola new species

Very suggestive of *pinicola* but slightly larger and more elongate, differs in the prominent exserted hairs on antennae and in the structure of the genital claspers.

♂. Length 6.4 mm. *Head*: width 1.11 mm., vertex .48 mm., length .6 mm.; carina obsolete but the vertex slightly impressed; marked very similarly to *pinicola* but the black arc each side of median line rarely connects with the black at base of tylus, the eyes also being slightly larger and more prominent. *Rostrum,* length 2.22 mm., scarcely attaining the posterior margins of the middle coxae, piceous, paler at the joints.

Antennae: segment I, length .51 mm.; II, 1.77 mm., nearly cylindrical but slightly tapering at base, equal in thickness to segment I, pale to dusky pubescent, exserted hairs prominent, in length equal to one and one-half times thickness of segment; III, .69 mm.; IV, .57 mm.; black, more or less shining.

Pronotum: length 1.42 mm., width at base 2.28 mm., anterior angles 1 mm.; collar .75 mm., opaque, brownish to black; disk moderately convex, coarsely black punctate, more deeply and irregularly behind the calli and at the sides; lateral margins irregularly defined, delimited by coarse punctures, a few pubescent hairs scattered along the margins, anterior angles narrowed, little wider than the collar; calli convex, confluent, black and shining, delimited behind by coarse punctures, the black color extending to front margin of disk except for a small spot before the lateral angles and one between at the median line; disk becoming piceous or black between the punctures, usually paler along the median line and behind lateral margins of calli; propleura more or less pale, black surrounding dorsal half of coxal cleft, opaque, black punctate but more

coarsely near the dorsal margin; xyphus nearly flat, infuscated on the disk, pale pubescent. *Scutellum* moderately convex, shining, impunctate but transversely rugulose on basal half, minutely pubescent, black, basal angles and apex pale to ivory-white, apical half of median line frequently pale; mesoscutum moderately exposed, black, minutely pubescent. *Sternum* black, opaque, median line and spot at base of middle coxae pale; pleura black, margins of sclerites more or less pale, opaque except for spot at dorsal margin of meso- and meta-episterna; ostiolar peritreme white, slightly infuscated at dorsal margin.

Hemelytra: width 2.74 mm., elongate, embolar margins nearly parallel, moderately convex; background pale translucent, coarsely and irregularly black punctate, corium with spot at base, middle, and irregularly across apex, outer edge and tip of embolium, black. *Cuneus* rather elongate, moderately deflexed, pale, black punctate, the apical half black. *Membrane* distinctly elongated, strongly infuscated, spot at tip of cuneus and extending more or less to the middle, within the areoles except at margins, pale; veins more heavily infuscated, the dark color invading the membrane somewhat on each side.

Legs: fuscous to blackish, tips of coxae and the trochanters paler; basal half of hind femora more or less pale, two or three rows of fuscous points persisting on the anterior face; tibiae biannulate with pale, frequently obscured with reddish or brownish; claws not at all cleft, dusky translucent, arolia similar to those of *pinicola*.

laricicola

Fig. 28. *Deraeocoris laricicola*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: black, shining, clothed with prominent pale pubescence; in paler forms flecked with reddish, the genital segment, more or less at base and a row of spots on sides, black; genital claspers (fig. 28) distinctive of the species.

♀. Length 6.1 mm., width 2.85 mm.; very similar to the male in coloration but in form less elongate; segment II, length 1.74 mm., moderately slender, thickened on the apical one-fourth but scarcely attaining the thickness of segment I, exserted hairs very prominent, length of those on basal half equal to three times the thickness of segment at middle, pubescence restricted chiefly to the enlarged apical one-fourth; III, .71 mm.; IV, .57 mm., all the segments black; venter brownish to black, in paler forms the black color develops first as a lateral line below the spiracles, on the genital segments and vagina exterior, the paler parts tinged with reddish.

Holotype: ♂ June 27, Ithaca, New York (H. H. Knight); author's collection. *Allotype*: taken with the type. Paratypes: 26♂ 29♀ taken with the types on *Larix laricina*, from the trees which grow on the north slope of the water reservoir on the Cornell University campus. MINNESOTA,—♂ July, 1914, Lake Itasca (S. A. Graham). NEW YORK,—♂ June 23, 2♂ July 1, 2♀ July 7, 1♂ 5♀ July 14, Batavia; ♂ June 16, ♂ June 28, 6♂ 6♀ July 2, Ithaca (H. H. Knight).

The writer has found this species only on *Larix laricina* to which tree the species is probably restricted in its breeding habits. The nymphs are dark colored, clothed with numerous bristles, but not coated with the white, wax-like material as is the case with the nymphs of *pinicola.* Fifth-stage nymphs were reared to the adult stage in cages, both nymphs and adults sucking sap from the tender larch shoots. The species may be predaceous to a certain extent but this point was not determined. It is interesting to note that the closely related but larger European species, *D. annulipes* H. S., lives on larch *(L. decidua)* also. Duda (1885), in some detailed observations on *D. annulipes* H. S. in Bohemia, states that the nymphs fed on aphids which were abundant on larch trees.

Deraeocoris kennicotti new species

Very much resembling and closely related to *laricicola* but having the dorsum distinctly hairy; structure of the male genital claspers very distinctive.

♂. Length (from collar to tip of membrane) 6.7 mm. *Head*: (missing in the only available male). ♀. Width 1.06 mm., vertex .5 mm., length .65 mm.; front and lower part of face closely and rather longly pubescent, tylus more prominent than in *laricicola;* vertex ecarinate, collum broadly exposed, black and shining, separated from vertex by a groove; testaceous, bordering inner margin of eye and projecting upon vertex, an arc each side of front composed of transverse bars but not attaining base of tylus, spot at base and geminate mark on basal half of tylus, juga, lorae, genae and bucculae, black. *Rostrum,* length 2.07 mm., nearly attaining hind margins of middle coxae, dark brownish to piceous, basal segment except narrow tip black.

Antennae: (♀) segment I, length .45 mm., testaceous, becoming black on basal half; II, 1.58 mm., moderately slender, becoming thickened on apical one-fourth but not attaining the thickness of segment I, rather closely beset with exserted hairs which in length are equal to twice thickness of segment at middle, testaceous, apical one-fourth blackish; III, .6 mm.; IV, .54 mm.; last two segments brownish to blackish.

Pronotum: length 1.34 mm., width at base 2.14 mm., anterior angles .8 mm., collar .63 mm.; disk moderately convex, punctures moderately coarse and rather closely set, distinctly hairy, longest near lateral and anterior margins; lateral margins fairly distinct, nearly straight, anterior angles narrowed to little wider than collar; calli moderately convex, irregularly delimited behind by coarse punctures, separated at basal margin by a pair of deep punctures, black, shining, pale between and just before, black color extending from latero-anterior angles to front margin of disk; disk grayish testaceous, punctures black, dark color working out from the punctures; propleura testaceous, black and opaque surrounding dorsal half of coxal cleft, punctures grouped chiefly on the dorsal half; xyphus nearly flat, pale pubescent, disk infuscated. *Scutellum* convex, transversely rugulose on basal half, longly pubescent or hairy, black, basal angles and apex pale, median line slightly indicated near apex. *Sternum*

and pleura black, opaque except for spot at dorsal margin of meso- and meta-episterna; ostiolar peritreme pale, invaded by fuscous at dorsal margin.

Hemelytra: width 2.8 mm., elongate, embolar margins nearly parallel; moderately convex, rather closely and uniformly black punctate, longly pubescent or hairy; background pale testaceous, translucent, dark color spreading from the punctures, spot at base, middle and more or less broadly at apex of corium, narrow edge and tip of embolium, apex of clavus, dark fuscous to blackish. *Cuneus* elongate, brownish black on apical half, paler and black punctate basally. *Membrane* infuscated, paler within the areoles and a spot bordering tip of cuneus which extends transversely more or less toward middle, veins dark fuscous.

Fig. 29. *Deraeocoris kennicotti*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Legs: fuscous to blackish, trochanters and tips of coxae paler; hind femora pale on basal half except for two or three rows of fuscous points, an obscure pale annulus on the apical half; tibiae biannulate with pale; tarsi blackish, structure of claws and arolia similar to those in *laricicola*.

Venter: dark brownish black, heavily pubescent; genital claspers (fig. 29.) distinctive of the species.

♀. Length 5.7 mm., width 2.75 mm.; more robust and the hemelytra shorter but in coloration very similar to the male (head and antennae described above).

♂. *Holotype*: "Great Slave Lake" [Canada] (Robert Kennicott); Uhler collection; Cat. No. 24175 U. S. N. M. *Allotype*: August 21, Mount Katahdin (alt. 5,300 ft.), Maine (C. P. Alexander); author's collection. *Paratype*: ♀, taken with the allotype.

This species is named in honor of Robert Kennicott, one of the pioneer collectors in northwestern America. The female is described from material collected on Mount Katahdin and thus widely isolated from the type locality but the specimens agree so closely, and the characters are so distinctive, there seems to be little doubt regarding their identity.

Deraeocoris fulvescens (Reuter)

1909 *Camptobrochis (Euarmosus) fulvescens* Reuter, Acta Soc. Sci. Fenn., xxxvi, No. 2, p. 56.

1917 *Camptobrochys (Euarmosus) fulvescens* Van Duzee, Cat. Hemip., p. 365.

Grayish testaceous to brownish, hemelytra semitranslucent, apical half of corium becoming piceous; dorsum pilose, lateral and anterior margins of pronotum distinctly hairy.

♂. Length 5.3 mm. *Head*: width 1.05 mm., vertex .51 mm., length .6 mm.; shape of head nearest to *barberi*, facial angle less than a right angle; carina obsolete, collum broadly exposed, black and shining, separated from

vertex by a groove; front broadly convex, shining, finely pilose; pale to testaceous and brownish, bordering front margin of eye, transverse bars each side of front and fusing below in a spot at base of tylus, slender apex and geminate mark on tylus, juga, dorsal margin of lorae, spot beneath eye and more or less at base of bucculae, black or brownish black. *Rostrum,* length 2.37 mm., reaching upon middle of hind coxae, brownish, becoming piceous at base and apex.

Antennae: segment I, length .35 mm., brownish; II, 1.28 mm., tapering gradually larger from base toward apex but scarcely attaining the thickness of segment I, yellowish to brownish, darker on the apical one-fourth, pale pubescent, length of exserted hairs equal to twice greatest thickness of segment; III, .54 mm.; IV, .45 mm.; last two segments brownish to fuscous.

Pronotum: length 1.25 mm., width at base 1.54 mm., anterior angles 1 mm., collar .74 mm.; disk moderately convex, coarsely black punctate, lateral margins distinct, slightly sinuate, anterior angles slightly rounded; calli moderately convex, separated at basal margin by a pair of deep punctures, dark brownish to black, basal margin with a projecting spot at lateral angle, a black arc extending from antero-lateral angle to front margin of disk; disk grayish testaceous and darkened with brownish, shining, pale just before the calli; propleura testaceous, finely black punctate, black just above and in front of coxal cleft; xyphus slightly convex, infuscated, longly pale pubescent. *Scutellum* convex, shining, sometimes transversely rugulose on basal half, clothed with long pilose hairs, brownish black, basal angles and apex pale or ivory-white, the median line sometimes palely indicated on apical half. *Sternum* and pleura dark brownish to blackish, pleural sclerites usually more or less pale around the margins; ostiolar peritreme white, sometimes becoming yellowish.

Hemelytra: width 2.48 mm., embolar margin slightly arcuate; moderately convex, clothed with erect pilose hairs, yellowish brown, somewhat translucent, punctures black, apical half of corium becoming piceous in well-matured specimens. *Cuneus* yellowish translucent, punctures infuscated, apical half dark brownish to blackish. *Membrane* pale to fumate, apical half, veins, and more or less invading membrane each side, infuscated.

Legs: thickly clothed with prominent erect hairs, reddish brown, tips of coxae, trochanters, and bases of femora paler; hind femora with a pale band before apex but usually incomplete on lower side; tibiae with a distinct pale annulus on apical half, two narrow and poorly defined pale annuli on the basal half, the pale band at middle of basal half usually incomplete on the dorsal side, the dark color usually distinctly reddish; tarsi brownish black, claws simple; arolia bristle-like, translucent, erect, inclined slightly forward, nearly parallel but converging slightly at tips.
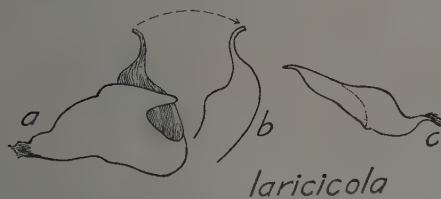

Fig. 30. *Deraeocoris fulvescens,* male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: dark reddish brown to blackish, shining, longly pale pubescent; genital claspers (fig. 30) distinctive of the species.

♀. Length 5.2 mm., width 2.4 mm., very similar to the male in form and slender, enlarged slightly at apex, rather 1.34 mm., color; segment II, length

sparsely beset with long erect hairs which in length are equal to three times the greatest thickness of segment, yellowish to brownish, slightly darker at apex; venter testaceous to reddish or dark brown, a row of impressed black spots, each side on the lateral submargin.

Allotype: ♂ July 24, 1900, Salida, Colorado; type material; author's collection. *Specimens examined*: ARIZONA,—♂ Aug. 3, Grand View, Grand Canyon (H. H. Knight). COLORADO,—2♂ 4♀ July 24, 1900, Salida; specimens collected with the type. NEW MEXICO,—♂ Aug. 3, ♂ Aug. 5, Las Vegas (Barber & Schwarz).

This species should be looked for upon pines in the Rocky Mountain region.

Deraeocoris pilosus new species

Very similar and closely related to *fulvescens*, but slightly larger and more uniformly colored; hemelytra uniformly reddish brown, not darker on the apical half of corium than on the embolium, tibiae triannulate with pale.

♂. Length 6.2 mm. *Head*: width 1.11 mm., vertex .52 mm., length .63 mm.; front and tylus more broadly blackish than in *fulvescens*. *Rostrum*, length 2.57 mm., nearly attaining posterior margins of hind coxae, brownish to piceous.

Antennae: segment I, length .37 mm., fusco-brownish; II, 1.4 mm., tapering from slender at base to thicker, the apical one-third equaling segment I in thickness, pale pubescent, length of exserted hairs equal to twice the thickness of segment, fusco-brownish, slightly darker at apex; III, .54 mm.; IV, .48 mm.; last two segments blackish.

Pronotum: length 1.34 mm., width at base 2.28 mm., anterior angles 1.08 mm.; collar .85 mm., brownish black, opaque; disk more closely punctate than in *fulvescens*, distinctly hairy; calli brownish black, the disk of each callus invariably paler than at the margins. *Scutellum* more flattened than in *fulvescens*, longly pilose, brownish black, basal angles and apex pale. *Sternum* and pleura brownish black; ostiolar peritreme largely infuscated or brownish.

Hemelytra: width 2.62 mm.; uniformly reddish brown, semitranslucent, rather closely and uniformly black punctate, clothed with prominent erect pilose hairs, apical half of corium never piceous as in *fulvescens*. *Cuneus* colored similarly to the corium, frequently more reddish on the apical half. *Membrane* uniformly pale fuscous or brownish, a slightly paler spot near tip of cuneus, veins frequently reddish brown.

pilosus

Fig. 31. *Deraeocoris pilosus*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Legs: reddish brown, marked with pale very similarly to *fulvescens* but the tibiae distinctly triannulate with pale.

Venter: dark reddish brown to piceous, shining, longly pale pubescent; genital claspers (fig. 31) indicate a close relationship with *fulvescens* but the right clasper and the internal arm of the left, exhibit specific differences.

♀. Length 5.8 mm., width 2.8 mm., very similar to the male in color but in form less elongate; segment II, length 1.37 mm., slender, enlarged slightly at apex, beset with prominent exserted hairs as in *fulvescens,* brownish, infuscated on the thickened apex.

Holotype: ♂ July 26, Mt. Lemon, alt. 9,000 ft., Santa Catalina Mts., Arizona (H. H. Knight); Cornell University collection. *Allotype*: taken with the type. *Paratypes*: ARIZONA,—4 ♂ 6♀ taken with the types on pine at the top of Mt. Lemon. 6 ♂ 10♀ July 29, Huachuca Mts., alt. 9,000 ft. (H. G. Barber).

The writer took specimens by beating a long-leaved pine, *Pinus arizonica.*

Deraeocoris nigritulus new name

1909 *Camptobrochis (Euarmosus) nigrita* Reuter, Acta Soc. Sci. Fenn., xxxvi, No. 2, p. 55. (name preoccupied)

1917 *Camptobrochys (Euarmosus) nigritus* Van Duzee, Cat. Hemip., p. 355.

Subovate, hemelytra only slightly convex, dorsum distinctly hairy, legs thickly clothed with long erect hairs; dark sepia brown to blackish, the subtranslucent parts stained with brownish.

♂. Length 5.9 mm. *Head*: width 1.14 mm., vertex .57 mm., length .68 mm.; front broad, moderately convex, carina very slight or not apparent, collum broadly exposed, separated from vertex by a groove; heavily pubescent, dark brownish black, tylus frequently paler and exhibiting two dark vittae, narrow basal margin of vertex and spot on juga frequently pale. *Rostrum*, length 2.28 mm., reaching slightly beyond hind margins of middle coxae, brownish black.

Antennae: segment I, length .51 mm.; II, 1.71 mm., slender, slightly enlarged on the apical one-fourth but not attaining thickness of segment I, dusky pubescent, length of exserted hairs equal to three times thickness of segment; III, .65 mm.; IV, .54 mm.; all the segments brownish black.

Pronotum: length 1.4 mm., width at base 2.42 mm., anterior angles 1.03 mm., collar .85 mm.; disk moderately convex, coarsely but rather uniformly punctate, distinctly hairy, lateral margins carinate, anterior angles distinct; calli convex, confluent, more blackish than pronotal disk; propleura more finely punctate than disk, lower margins slightly paler; xyphus nearly flat, testaceous to brownish. *Scutellum* moderately convex, smooth and shining, pilose, brownish black. *Sternum* and pleura dark brownish black, dull except for the small spots at dorsal margins of the episterna; ostiolar peritreme pale brownish to blackish.

Hemelytra: width 2.9 mm., embolar margin moderately arcuate; slightly convex, clothed with long brownish pilose hairs, rather coarsely and closely black punctate; sepia brown to blackish, embolium semitranslucent but stained with brownish. *Cuneus* uniformly colored like the corium. *Membrane* and veins fusco-brownish, slightly paler immediately distad of the areoles and opposite tip of cuneus.

Legs: dark brownish to blackish, shining, tips of coxae, trochanters, and bases of femora paler; tibiae rather broadly but sometimes obscurely annulated with paler on the apical half, rather thickly beset with prominent erect hairs which in length exceed thickness of tibia; tarsi fusco-brownish, claws with a slight indication of a notch (fig. 2, C); arolia slender, bristle-like, erect, directed slightly forward, converging at the apices.
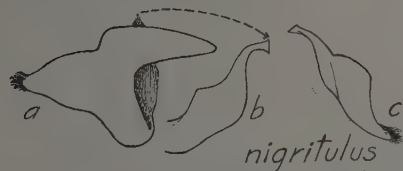
Fig. 32. *Deraeocoris nigritulus*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: brownish black, shining, clothed with prominent brownish pubescence; genital claspers (fig. 32) distinctive of the species.

♀. Length 6.4 mm., width 3.1 mm.; very similar to the male in form and color; segment II, length 1.85 mm., slender, very slightly thickened at apex, beset with exserted hairs which in length are equal to three times thickness of segment, fusco-brownish, darker at apex.

Lectotype: ♂ June 25, 1895 (!), Washington, D. C. (O. Heidemann); Cat. No. 24170 U. S. N. M. *Allotype*: ♀ July 2, Washington, D. C. (Wm. T. Davis); author's collection. *Plesiotype*: ♂ June 27, Great Falls, Virginia (Wm. T. Davis); compared with type; author's collection. *Specimens examined*: DISTRICT OF COLUMBIA,—♂♀ May 20 to July 24, Washington (O. Heidemann). 2♂ 2♀ May 21, Petworth. 2♀ June 22, Washington (Wm. T. Davis). MARYLAND,—33♂♀ May 9, ♂ May 18, ♂ 3♀ June 8, corner Conduit and Potomac roads, on *Pinus virginiana;* ♂ May 28, 2♀ June 15, Beltsville; ♀ June 20, Odenton; 2♂ June 17, Plummers Island (W. L. McAtee). 2♀ May 24, Glen Echo (P. R. Uhler). ♀ June 15, Cabin John Run (Wm. T. Davis). ♀ July 6, Blandensburg; ♀ July 3, Forest Glen (O. Heidemann). VIRGINIA,—3♀ May 31, Four Mile Run (W. L. McAtee), ♀ May 28, Dyke. 3♀ May 30, 1883, "Va. on pine" (Pergande).

Both Heidemann and Mr. McAtee have found this species to breed on *Pinus virginiana.*

Deraeocoris albigulus new species

Closely related to *nigritulus* but differs slightly in coloration and in the structure of the male genital claspers; dark fuscous to black, basal half of hemelytra more or less pale between punctures, the paler areas not stained with brownish.

♂. Length 6.5 mm. *Head*: width 1.22 mm., vertex .55 mm., length .63 mm.; vertex slightly impressed at each side and thus causing a slight carina at basal margin; pale pubescent, black, gula and lower half of genae, sides of

tylus, spot on lorae, basal angles of juga, arcuated streak each side of front, basal margin of vertex, pale. *Rostrum,* length 2.51 mm., reaching to middle of hind coxae, piceous.

Antennae: segment I, length .48 mm., black; II, 1.68 mm., more slender on basal half and gradually enlarged toward apex, nearly attaining thickness of segment I, pubescence infuscated, length of exserted hairs greater than thickness of segment, black, more brownish on the basal one-third; III, .63 mm.; IV, .57 mm.; last two segments blackish.

Pronotum: length 1.54 mm., width at base 2.45 mm., anterior angles 1.03 mm.; collar .85 mm., black, opaque; disk and calli black, slenderly pale at basal margin, in paler forms the disk may be fusco-grayish between the punctures; lateral margins more nearly straight and the anterior angles more sharply defined than in *nigritulus;* propleura black, lower margins pale; xyphus nearly flat, pale, a dark mark at anterior angles. *Scutellum* moderately convex, shining, longly pale pubescent, black, basal angles and apex pale; mesoscutum moderately exposed, black, pubescent. *Sternum* and pleura black, opaque; ostiolar peritreme pale, infuscated at dorsal margin, sometimes tinged with reddish.

Hemelytra: width 2.9 mm., structurally very similar to *nigritulus;* fuscous to black, black color spreading from the punctures, clavus and basal half of embolium and spot on corium paler between the punctures, not stained with brown as in *nigritulus,* apical half of corium and apex of clavus piceous. *Cuneus* black, paler between punctures on basal half. *Membrane* heavily infuscated on the apical half, a ray projecting basally between the areoles, veins and slightly invading the membrane either side dark fuscous, the paler areas bordering the brachium and within the areoles fumate.

Legs: dark brownish black, in paler forms the hind tibiae indistinctly annulated with paler on the apical half; hairs on tibiae less prominent than in *nigritulus;* structure of claws and arolia very similar to those of *nigritulus.*
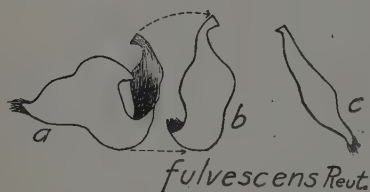

Fig. 33. *Deraeocoris albigulus,* male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: black, shining, dusky pubescent; genital claspers (fig. 33) distinctive of the species, closely related to *nigritulus* but exhibiting specific differences.

♀. Length 7.1 mm., width 3.1 mm.; very similar to the male in form and color; segment II, length 1.94 mm., slender, thickened on the apical one-fourth but scarcely attaining the thickness of segment I, pubescence infuscated, length of exserted hairs about equal to twice greatest thickness of segment, fusco-brownish, the apical one-fourth black.

Holotype: ♂ June 30, Ithaca, New York (H. H. Knight; author's collection. *Allotype:* taken with the type on *Pinus sylvestris. Paratypes:* INDIANA,—2♂ 1♀ June 27, ♀ July 4, Miller (W. J. Gerhard). MICHIGAN,—3♀ June, Huron Mt. Club, Lake Superior (H. G. Barber). 1♂ 1♀ July 30, Marquette. NEW YORK,—♀ June 22, 2♀ June 30, 2♀ July 8, Ithaca (H. H. Knight), taken on *Pinus sylvestris.*

The writer has found nymphs and adults on *Pinus sylvestris* but the species will doubtless be found on *Pinus resinosa* also, a supposition based on the fact that three other species of Miridae, *Phytocoris pinicola* Knight, *Pilophorus sp.* and *Psallus sp.* were found to be breeding on both these pines. Since *Pinus sylvestris* is supposed to have been introduced from Europe in recent times, the species of Miridae mentioned must have bred originally only on *Pinus resinosa* for it seems quite certain these insects are not known from Europe at the present time.

KEY TO THE SPECIES OF GROUP VI

1. Hemelytra uniformly black or sepia black, the embolium sometimes pale; cuneus frequently translucent but not distinctly paler on the basal half than apex 2
   Hemelytra not uniformly black, testaceous to dark brownish, or with background pale to grayish and darkened with blackish, sometimes rufo-piceous *(rufiventris)* but in such case the cuneus is distinctly paler on the basal half; cuneus pale or reddish at least on the basal half . 4

2. Head pale along the median line of front, transversely marked with black at each side; femora brownish black, indistinctly annulated with paler near the apices . . . *comanche* n. sp. p. 177
   Head black along the median line of front or the front entirely pale, never transversely marked with black at each side of the median line; femora largely pale or entirely black, rarely annulated as the above . 3

3. Femora pale, a broad piceous annulation on the apical half; median line of frons broadly black, also black along front margin of eyes; disk of pronotum pale at the lateral margins, the median line not indicated; scutellum with never more than median line pale . . . .
   . . . . *apache* n. sp. p. 179
   Femora black, sometimes with a pale annulation on the apical half, if pale on the basal half then also pale along front margin of eyes; pronotal disk frequently pale at the lateral margins but in such case the median line is also indicated in pale; scutellum frequently pale or

4. Front of head pale or reddish, if marked with black then the calli pale and lined with black; the pronotum largely pale or fulvous . . 6
   Front of head marked with black, the calli solid black or nearly so . 5
   . . . . *fusifrons deletans* n. var. p. 181

5. Hind femora with two reddish brown bands on the apical half, tibiae annulated with brownish black at near middle, the apices broadly darkened with brown; venter piceous . . *fusifrons* n. sp. p. 180
   Hind femora with one dark brown band on the apical half, tibiae indistinctly annulated; venter testaceous, each side with a row of rounded, impressed, polished brownish black spots, one on each segment situated slightly beneath the spiracle . . . .
   reddish . . . . *sayi* Reut. p. 174

6. Calli largely pale and lined with black, or largely black and marked
    with pale . .   .   .   ,   . . ,   .   .   .   8
    Calli solid black   7

7. Dorsum rufo-piceous, cuneus reddish on the basal half; legs and ven-
    tral surface largely reddish, tibiae triannulate with pale .   .   .
    .   .   .   . ·rufiventris n. sp. p. 184

    Dorsum more or less pale yellowish to brownish, each hemelytron
    broadly piceous at apex of corium and again with a smaller blotch at
    the middle, cuneus pale on basal half; legs and ventral surface yel-
    lowish, tibiae and apical half of femora banded with reddish or
    piceous   .   .   .   . fenestratus Van D. p. 182

8. Legs reddish, tibiae paler and biannulate with reddish brown on the
    basal half; disk of pronotum fulvous, becoming darker toward the
    basal margin; hemelytra with background pale to brownish, apex dark
    brown to piceous, a smaller blotch at middle and in dark specimens
    this may unite with the black apical area   . vanduzeei n. sp. p. 183
    Legs pale or yellowish, hind tibiae usually banded with brown near
    middle, also an incomplete brown annulus on apical half of femora;
    pronotum pallid to testaceous, frequently becoming darker on the sub-
    basal margin   9

9. Pronotal disk sparsely pubescent, coarsely, irregularly, and deeply punc-
    tate; calli distinctly swollen; elongate, dorsum rather sparsely beset
    with hairs; dark coloration with a decidedly rich brownish cast .   .
    .   .   .   .   cerachates Uhler p. 187
    Pronotal disk distinctly hairy, more finely and rather closely punc-
    tate; calli nearly flat, beset with a few hairs; form more ovate, dorsum
    and legs distinctly hairy; dark coloration fuscous to blackish ..   .   10

10. Scutellum pale or yellowish brown   11
    Scutellum marked with black   .   ·   12

11. Ground color chiefly honey yellow, scutellum yellowish brown, pro-
    notal disk finely and rather closely punctate   .   .   .   .   .
    .   .   .   . californicus n. sp. p. 185
    Ground color pallid and more or less bleached, pronotal disk apparently
    more coarsely and sparsely punctate   .   .   .   .
    .   .   .   .   .   . californicus desiccatus n. var. p. 187

12. Cuneus pale, darkened at apex; frons pale to yellowish   .   .   .
    .   .   .   . californicus bradleyi n. var. p. 187
    Cuneus sanguineous, paler at outer margin; frons transversely marked
    · with black each side of median line .   .   .   .
    .   .   .   .   .   . californicus rufocuneatus n. var. p. 187

Deraeocoris sayi (Reuter)

1876 *Euarmosus Sayi* Reuter, Ofv. Kongl. Sv. Vet.-Akad. Forh., xxxii, No. 9,
    p. 76.
1909 *Camptobrochis (Euarmosus) sayi* Reuter, Acta Soc. Sci. Fenn., xxxvi,
    No. 2, p. 55.
1917 *Camptobrochys (Euarmosus) sayi* Van Duzee, Cat. Hemip., p. 355.

Key to the Varieties of Sayi

Deraeocoris sayi sayi (Reuter)

♂. Length 7.4 mm. *Head*: width 1.25 mm., vertex .6 mm., length .68 mm.; carina slight but apparent, collum broadly exposed, pale, separated from vertex by a groove; front broad and only slightly convex; facial angle a right angle or slightly greater, juga prominent, face strongly pubescent; pale to yellowish, surrounding base of antenna, lorae, bucculae, tip of tylus and sometimes a geminate mark on basal half, fuscous to blackish. *Rostrum*, length 2.34 mm., nearly attaining hind margins of the middle coxae, dark brownish to piceous.

Antennae: segment I, length .6 mm.; II, 1.77 mm., nearly cylindrical but tapering smaller at base, equal in thickness to segment I, dusky pubescent, length of exserted hairs about equal to twice the thickness of segment; III, .62 mm.; IV, .43 mm.; all the segments black.

Pronotum: length 1.6 mm., width at base 2.82 mm., anterior angles 1.14 mm.; collar .91 mm., yellowish brown; disk moderately convex, rather closely but more coarsely punctate behind the calli, lateral margins distinct, nearly straight, anterior angles narrow but distinct, strongly pubescent or hairy; black, slender basal margin, narrowly at anterior angles, and median line on disk near posterior margin, pale; calli very slightly convex, black, smooth and shining; propleura black, opaque except at dorsal margin, becoming pale at lower margin, more finely punctate than disk; xyphus nearly flat, pale to yellowish, finely pubescent. *Scutellum* moderately convex, pilose, yellowish to pink or red, the median line frequently paler; mesoscutum moderately exposed, blackish. *Sternum* fusco-brownish to black, paler at the median line; pleura blackish, paler at margins of sclerites; ostiolar peritreme dark fuscous.

Hemelytra: width 3.4 mm., embolar margin slightly arcuate; disk moderately convex, strongly pubescent or hairy, coarsely and rather closely punctate; uniformly black or brownish black. *Cuneus* moderately deflexed, black like the corium. *Membrane* and veins strongly infuscated, paler bordering tip of cuneus and apex of areoles.

Legs: black, femora indistinctly marked with a pale annulus before apex, prominently clothed with long erect hairs; tibiae black, annulated with pale at middle of basal half and more broadly at middle of apical half, thickly clothed with prominent erect hairs which in length nearly equal twice the thickness of tibia; tarsi fusco-brownish, blackish at tips; claws (fig. 2, D) deeply cleft, brownish to piceous; arolia slender, bristle-like, erect but inclined slightly forward, converging slightly at the apices.
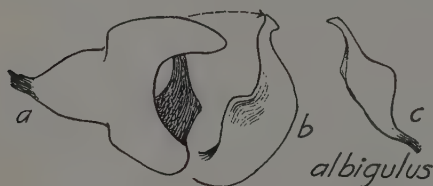

Fig. 34. *Deraeocoris sayi*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: black, shining, clothed with yellowish pubescence; genital claspers (fig. 34) distinctive of the species.

♀. Length 7.9 mm., width 3.8 mm., usually larger than the male but very similar in form and coloration; segment II, length 1.99 mm., slender, slightly thickened apically but not attaining the thickness of segment I, rather thickly clothed with prominent erect hairs, length of longest hairs equal to three times the thickness of segment at middle, fusco-brownish, black on the apical one-fourth.

Plesiotype: ♂ "Texas"; author's collection. *Specimens examined*: ALABAMA,—♂ April 5, Mobile (H. P. Loding). ILLINOIS,—♂ June 19, Glen Ellyn (W. J. Gerhard), on oak. MINNESOTA,—♀ July 2, St. Paul (A. A. Nichol). NEW YORK,—♀ June 14, Ithaca (H. H. Knight). NORTH CAROLINA,—♀ May 2, Raleigh (R. W. Leiby). TEXAS,—♀ April 11, 1♂ 1♀ May 20, Victoria (J. D. Mitchell), on live oak, *Quercus virginiana*.

In the original description Texas was cited as the type locality, but *sayi* with its color varieties is widely distributed in the eastern United States altho usually scarce in collections. Data on the above collectors' labels indicate that the species may be found most frequently on oaks.

Deraeocoris sayi marginatus new variety

Similar to the typical *sayi* but differs in being more broadly pale or reddish; lateral margins of pronotal disk broadly pale or reddish.

Holotype: ♂ June 9, Chicago, Illinois (W. J. Gerhard), at light; author's collection. *Paratypes*: FLORIDA,—3♀ April 18, St. Augustine (C. W. Johnson). GEORGIA,—♂♀ April 22 to May 12, St. Simon Island (J. C. Bradley). MICHIGAN,—♀ "Mich."

Deraeocoris sayi frontalis new variety

Differs from the typical *sayi* as indicated in the key; black, scutellum and mark on median line at base of pronotal disk pale or reddish, front of head and lower part of face largely blackish; tibiae biannulate with pale as in the typical form.

Holotypte: ♂ June 19, Glen Ellyn, Illinois (W. J. Gerhard), on oak; author's collection.

Deraeocoris sayi costalis new variety

Similar to the typical *sayi* but differs as indicated in the key; hemelytra with costal margin and cuneus largely pale, lateral margins of pronotal disk also pale.

Holotype: ♂ June 19, Pine Island, New York (Wm. T. Davis); author's collection.   *Paratypes*:   ILLINOIS,—♀ June 12, Galesburg (Stromberg).   MASSACHUSETTS,—♀, Waltham.

Deraeocoris sayi femoralis new variety

Apparently not differing structurally from the typical *sayi* but very dissimilar in color aspect; black, cuneus except narrowly at base, and the slender costal margin pale translucent; median line of pronotal disk slightly pale near base, scutellum pale only on median line near apex; head largely black as in *frontalis;* legs largely pale, femora with a broad blackish band at middle of apical half, a series of fuscous points on the basal half; tibiae triannulate with blackish, the apical band sometimes much reduced.

Holotype: ♂ June 17, Norman County, Minnesota (A. A. Nichol); Minnesota University collection.   *Allotype*: taken with the type.

Deraeocoris sayi unicolor new variety

Apparently not differing structurally from the typical *sayi* but the dorsum uniformly black; head blackish as in *frontalis,* vertex and sides of front more or less pale.

Holotype: ♂ June 18, Glen Ellyn, Illinois (W. J. Gerhard); author's collection.   *Paratypes*:   ILLINOIS,—♂ June 9, Chicago; ♀ June 18, ♂ June 19, Glen Ellyn (W. J. Gerhard).   ♂ June 14, Galesburg (Stromberg).   WISCONSIN,—♀ June 23, Beaver Dam (W. E. Snyder).

Deraeocoris comanche new species

Closely related to *sayi* but smaller and more ovate; front of head transversely marked with black each side of the median line.

♂. Length 5.7 mm. *Head*: width 1.08 mm., vertex .54 mm., length .63 mm.; facial angle practically a right angle, carina obsolete; collum black, broadly exposed, separated from vertex by a deep groove; lower face strongly pubescent, juga less prominent than in *sayi;* testaceous to pale brownish, front transversely marked with black each side of the median line, forming two arcs which meet above at front margin of vertex; a triangular mark each side of vertex and one at base of tylus, geminate mark on basal half of tylus, lorae and bucculae, dark fuscous to black. *Rostrum,* length 2.11 mm., nearly attaining posterior margins of middle coxae, brownish to piceous, darker at base and apex.

Antennae: segment I, length .44 mm.; II, 1.74 mm., gradually enlarged from base toward apex, attaining the thickness of segment I, dusky pubescent, length of exserted hairs on basal half of segment equal to more than twice greatest thickness of segment; III, .48 mm.; IV, .43 mm.; brownish black, last two segments darker.

Pronotum: length 1.25 mm., width at base 2.14 mm., anterior angles 1.05 mm., collar .8 mm.; disk moderately convex, slightly sulcate and more coarsely punctate each side of the calli on the lateral submargin, lateral margins distinct, nearly straight, anterior angles prominent, black punctate and distinctly hairy; calli convex, a pair of punctures just between, scarcely distinguished posteriorly from the disk except at latero-posterior angles, black, pale just before but a black mark extending from lateral angles to front margin of disk; disk black, shining, broadly pale at lateral margins; propleura pale to brownish, black punctate, blackish dorsally surrounding the coxal cleft; xyphus slightly convex, infuscated, longly pale pubescent. *Scutellum* moderately convex, pilose, black, the apex pale; mesoscutum black, moderately exposed. *Sternum* and pleura brownish black, basalar plate and margins of sclerites yellowish brown; ostiolar peritreme pale, becoming brownish or even blackish at dorsal margin.

Hemelytra: width 2.65 mm., embolar margin moderately arcuate; disk moderately convex, coarsely and rather uniformly punctate, clothed with prominent pubescent hairs; brownish black, shining, spot at base of corium and one next to the cuneal fracture, and the basal half of the embolium, pale translucent. *Cuneus* punctate, pubescent, colored like the corium. *Membrane* and veins strongly infuscated, paler bordering apex of cuneus.

Legs: brownish black, thickly clothed with prominent erect pale hairs; femora with an indistinct pale annulus just before apex; tibiae pale at the knee and a narrow annulus on the basal half, becoming slightly paler at apices; claws and arolia similar to those of *sayi*.

Venter: brownish black or piceous, shining, yellowish pubescent; genital claspers (fig. 35) distinctive of the species.

♀. Length 6 mm., width 3 mm.; slightly larger and more ovate than the male but very similar in color; segment II, length 1.6 mm., slightly more slender than in
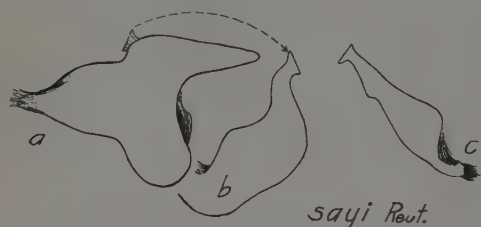

Fig. 35. *Deraeocoris comanche,* male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

the male, thicker at apex but not attaining the thickness of segment I, brownish black, length of exserted hairs equal to three times thickness of segment at middle.

Holotype: ♂ June 16, Williams, Arizona (Barber & Schwarz); Cat. No. 24167 U. S. N. M. *Allotype*: July 1, Williams, Arizona (H. Barber); Cornell University collection. *Paratypes*: ARIZONA,— ♀ June 7, Williams (Barber & Schwarz). 2♀ July 1, Williams (H. Barber). NEW MEXICO,—♀, "N. M."; Minnesota University collection.

Deraeocoris apache new species

Larger than *comanche,* femora pale but with a piceous annulation on the apical half.

♂. Length 7.2 mm. *Head*: width 1.22 mm., vertex .57 mm., length .74 mm.: front less vertical and the hind margin of the eyes more removed from base of head than in *comanche;* black, shining, narrow basal margin of vertex, large spot each side of front and usually connected with juga, tylus except for a geminate mark on basal half, gula, lorae and juga largely, yellowish. *Rostrum,* length 2.34 mm., reaching to middle of intermediate coxae, yellowish to brownish and becoming piceous at apex.

Antennae: segment I, length .6 mm., piceous; II, 1.88 mm., nearly cylindrical but slightly more slender near base, equal to segment I in thickness, dusky pubescent, length of exserted hairs equal to twice the thickness of segment, yellowish brown, brownish black on the apical one-third; III, .77 mm.; IV. .48 mm.; last two segments slender, brownish to fuscous.

Pronotum: length 1.57 mm., width at base 2.74 mm., anterior angles 1.17 mm.; collar .85 mm., dark brownish black, opaque; disk moderately convex; coarsely punctate, distinctly hairy, lateral margins distinct, nearly straight, anterior angles less prominent than in *comanche;* calli practically flat, slightly impressed at hind margins, a pair of widely set punctures just between, black and shining, pale just before, a black arc extending from antero-lateral angles to front margin of disk; brownish black or piceous, lateral margins of disk broadly pale but less broadly at basal angles; propleura pale or yellowish, punctures brownish, brownish black before and behind the coxal cleft; xyphus slightly convex anteriorly, brownish black, pale pubescent, the carinate margins bordering coxal cavities yellowish. *Scutellum* convex, pilose, smooth and shining, brownish black, the median line, basal angles, and apex pale, in paler forms the lateral margins may be pale from base to apex. *Sternum* brownish black, median line and margins yellowish, pleura yellowish brown, more or less brownish black on the disk of each sclerite, distinctly pilose; ostiolar peritreme pale to yellowish, dorsal margin slightly invaded with brownish.

Hemelytra: width 3.4 mm., embolar margin slightly sinuate; disk moderately convex, coarsely punctate, distinctly hairy, uniformly brownish black, shining. *Cuneus* brownish black, a small pale point at the outer basal margin. *Membrane* and veins fusco-brownish, slightly paler bordering the tip of cuneus.

Legs: pale and banded with piceous or black, distinctly hairy; femora

with a rather broad piceous band at middle of apical half, two series of fuscous points on anterior face of basal half, a secondary obsolete and more or less interrupted fuscous band just before apex; tibiae triannulate with brownish black, also a dark spot on the knee, thickly clothed with long erect hairs, length of longest hairs equal to twice the thickness of tibia; tarsi yellowish brown, darker at apices; claws and arolia similar to those of *sayi*.

Fig. 36. *Deraeocoris apache*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: brownish to piceous, paler at the sides, a series of impressed piceous spots on each side, one on each segment beneath the spiracle but somewhat removed from it; genital claspers (fig. 36) very distinctive of the species.

♀. Length 7.2 mm., width 3.4 mm.; very similar to the male in color and structure, the piceous band on femora much reduced and more brownish in color; segment II, length 1.85 mm., more slender than in the male, gradually enlarged toward apex, length of exserted hairs equal to more than three times the thickness of segment at middle, yellowish to brownish, dark brown on the apical one-fourth; segment I more reddish brown than piceous; membrane paler than in the male.

Holotype: ♂ June 20, Prescott, Arizona (H. S. Barber); Cat. No. 24168 U. S. N. M. *Allotype*: topotypic; Cornell University collection. *Paratypes*: ARIZONA,—♀ June 17, 2♀ June 19, ♂ 2♀ June 20, Prescott (H. S. Barber). ♂, "Ariz." (Uhler collection).

Deraeocoris fusifrons new species

Larger than *fenestratus*, frons marked with black, calli solid black, dorsum pale and darkened with piceous; femora pale, two reddish brown bands on the apical half.

♂. Length 6.4 mm. *Head*: width 1.14 mm., vertex .51 mm., length .65 mm.; facial angle slightly less than a right angle, structurally very similar to *fenestratus;* carina obsolete, collum black, broadly exposed, separated from the vertex by a groove, lower face strongly pubescent; pale to yellowish, bordering inner margin of eyes and projecting upon vertex, transverse marks on front each side of median line, geminate mark on basal half of tylus, spot beneath eye, dorsal half of bucculae, spot at base and the slender tip of tylus, piceous or black. *Rostrum*, length 2.19 mm., attaining hind margins of middle coxae, yellowish brown, piceous on basal segment and at apex.

Antennae: segment I, length .51 mm., yellowish brown; II, 1.6 mm., gradually enlarged from base toward apex, attaining the thickness of segment I, dusky pubescent, length of exserted hairs nearly equal to twice greatest thickness of segment, yellowish, the apical one-fourth blackish; III, .63 mm.; IV, .48 mm.; last two segments brownish to fuscous.

Pronotum: length 1.42 mm., width at base 2.42 mm., anterior angles 1.2 mm., collar .83 mm.; disk convex, coarsely but sparsely punctate, longly pubes-

cent or hairy, lateral margins distinct, nearly straight, anterior angles rounded but distinct; calli convex, subconfluent, black, invaded by pale at the latero-anterior angles from which a black arc extends to front margin of pronotal disk; disk testaceous, becoming piceous on the basal one-third each side of the median line, punctures piceous, more sparsely and irregularly placed just behind the calli; propleura testaceous to brownish, black punctate; xyphus slightly convex, infuscated, pale pubescent. *Scutellum* convex, smooth and shining, pilose, testaceous, black vitta each side of median line which fuse at base; mesoscutum moderately exposed, black, brownish at the lateral angles. *Sternum* brownish black, paler at the median line and around the margins, pleura yellowish to brownish; ostiolar peritreme pale to yellowish, a blackish spot just above.

Hemelytra: width 3 mm., embolar margin slightly arcuate; disk convex, coarsely black punctate, thickly clothed with prominent pubescent hairs; piceous or black, more or less pale between the punctures on the clavus, basal half of embolium, spot near base, and at apical inner angles of corium; more nearly black at tip of clavus, large spot on middle and broadly across apex of corium and embolium. *Cuneus* pale, apical half and narrowly at base black, punctures concolorous. *Membrane* fusco-brownish, slightly darker on veins and at either side, paler near tip of cuneus and basal half of areoles.

Legs; pale, vestiture of hairs shorter and less prominent than in *fenestratus;* femora with two reddish brown bands on apical half, interrupted below and on posterior face; tibiae with a brownish or piceous band at middle,

Fig. 37. *Deraeocoris fusifrons,* male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

the apices broadly darkened with brownish, clothed with suberect hairs which in length scarcely exceed thickness of tibiae; claws deeply cleft, arolia slender, bristle-like, erect, nearly parallel but converging slightly at apices.

Venter: dark brownish to piceous, yellowish pubescent; genital claspers (fig. 37) distinctive of the species.

Holotype: ♂ May, Santa Clara County, California (Coleman); author's collection. *Paratype*: ♂, taken with type.

Deraeocoris fusifrons deletans new variety

♀. Length 5.7 mm., width 3 mm. Structurally very similar if not identical with the typical *fusifrons,* also the piceous coloration of head and dorsum very similar but more broadly pale on hemelytra, embolar margin more distinctly arcuate; femora with only one dark brown band on anterior face of the apical half, tibiae indistinctly marked with brown at middle; venter testaceous, each side with a row of rounded, impressed, polished brownish black spots, one on each segment situated slightly beneath the spiracle; membrane pale fuliginous. *Antennae*: segment I, length .48 mm., yellowish brown; II, 1.57 mm.,

slender, gradually thickened toward apex but not attaining the thickness of segment I, length of longest exserted hairs equal to three times the greatest thickness of segment, yellowish, the apical one-fourth blackish; III, .65 mm.; IV, .45 mm.; last two segments brownish and darkened with fuscous.

Holotype: ♀ August, Marin County, California; Cornell University collection.

Deraeocoris fenestratus (Van Duzee)

1917 *Camptobrochis fenestratus* Van Duzee, Proc. Calif. Acad. Sci., ser. 4, vii, p. 266.

Length 5.5-6 mm. Suboval, yellowish to reddish and piceous, punctured and marked with black, shining; margins of pronotum and hemelytra hairy; front of head and vertex devoid of black marks.

Length 5.5 mm. *Head*: width 1.05 mm., vertex .51 mm., length .77 mm.; more produced than in *fulvescens,* front moderately convex, polished, carina obsolete, collum broadly exposed and elevated slightly above vertex, brownish; yellowish to reddish, geminate mark on basal half of tylus and narrowly at apex, epipharynx, dorsal margins of lorae and bucculae, piceous. *Rostrum*, length 2.4 mm., scarcely attaining posterior margins of hind coxae, first segment attaining base of head; brownish, basal segment reddish, the apical one piceous.

Antennae: segment I, length .48 mm., yellowish, slightly darker beneath, certain hairs equaling thickness of segment: II, 1.65 mm., slender, yellowish, the apical one-fourth slightly thicker and blackish in color, clothed with prominent pale hairs, length of several being three times the thickness of segment; III, .68 mm., yellowish; IV, .57 mm., slightly infuscated.

Pronotum: length 1.22 mm., width at base 2.17 mm.; anterior angles .94 mm., slightly rounded; collar .77 mm., finely granulate, brownish; disk pilose, distinctly hairy at lateral margins, yellowish to rich brownish, sub-basal areas becoming piceous (disk practically black in one specimen); punctures coarse, black, irregularly but not densely punctate; calli flat, black and shining, a piceous arc extending to anterior angles; propleura yellowish brown, in darkest specimens becoming piceous above, xyphus reddish. *Scutellum* impunctate, shining, somewhat pilose, piceous, basal angles and median line pale; mesoscutum brownish, scarcely exposed. *Sternum* and pleura brownish to reddish, dull; ostiolar peritreme pale but with some reddish.

Hemelytra: width 2.72 mm., convex, embolium arcuated from base to apex, cuneus and membrane deflexed; pilose, longest hairs on embolium; coarsely and irregularly punctate, punctures black; shining, yellowish to brownish, more or less translucent, corium broadly piceous at apex, more or less joined with a large spot at middle; embolium pale, piceous at apex and darkened along the extreme outer edge. *Cuneus* pale, inner basal angle and apical one-third piceous. *Membrane* fuliginous, darker bordering the veins, faintly paler at tip of cuneus and tending to become a transverse band; veins dark brownish.

Legs: pale yellowish to brownish, strongly pilose, long hairs on tibiae equal to at least twice the thickness of tibia; apical half of femora brownish or red-
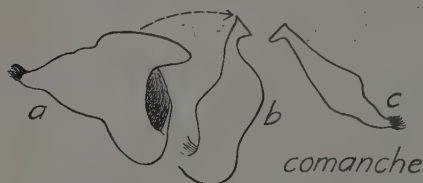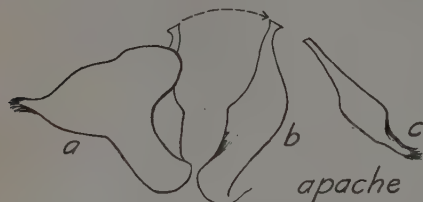
fenestratus VanD

Fig. 38. *Deraeocoris fenestratus*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

dish; indistinctly annulated with paler; tibiae pale, broadly banded at apex, middle, and more narrowly near base with brownish or reddish; tarsi pale, fuscous at apices.

Venter: reddish, shining, becoming piceous on the genital segment, strongly pilose; genital claspers (fig. 38) distinctive of the species.

♀. Length 5.7 mm., width 2.85 mm.; very similar to the male in all respects except the genital segment.

Plesiotype: *paratype,* ♂ Aug. 21, 1916, Fallen Leaf Lake, Eldorado Co., California (W. M. Giffard); collection of E. P. Van Duzee.

Specimens examined: paratype, same data as plesiotype. ♂♀, September, Placer Co., California.

Deraeocoris vanduzeei new species

Very suggestive of *fenestratus* but smaller, more ovate, calli marked with black; distinguished by the genital claspers, particularly in the form of the internal arm of the left clasper.

♂. Length .4.6 mm. *Head*: width .97 mm., vertex .48 mm., length .54 mm.; structurally nearly identical with *fenestratus;* yellowish brown and tinged with reddish, geminate mark on tylus nearly obsolete. *Rostrum,* length 1.88 mm., reaching upon middle of the hind coxae, brownish and tinged with red.

Antennae: segment I, length .4 mm., yellowish, darkened with reddish or brown; II, 1.28 mm., slender, thickened apically and nearly equaling segment I in thickness, the longest exserted hairs nearly equal to three times the greatest thickness of segment, yellowish, the apical one-third black; III, .6 mm.; IV, .45 mm.; last two segments yellowish to brownish.

Pronotum: length 1.08 mm., width at base 1.97 mm., anterior angles .85 mm., collar .68 mm.; disk convex, punctures much finer than in *fenestratus,* lateral margins distinct, nearly straight, anterior angles rounded and distinctly narrowed; calli slightly convex, brownish, front margin and somewhat between, line on the hind margin with recurved hook at latero-posterior angle, mark on disk of each which extends toward latero-anterior angle and frequently joins spot at front margin of pronotal disk, black; disk largely fulvous, darker near basal margin where the piceous coloration spreads from the punctures, beset with prominent pale pubescence, hairs longest at lateral margins and anterior angles; propleura yellowish, finely punctate; xyphus nearly flat, reddish, pale pubescent. *Scutellum* strongly convex, smooth and shining, margins pubescent, dark brownish black or piceous, basal angles broadly and the apex narrowly pale; mesoscutum slightly exposed, blackish, brownish at lateral angles. *Sternum* and pleura yellowish to reddish; ostiolar peritreme yellowish and tinged with reddish.

Hemelytra: width 2.48 mm., embolar margin strongly arcuated; disk convex, shining, finely pubescent, coarsely and rather irregularly black punctate; ground color pale to testaceous, piceous surrounding each puncture and spreading to connect in groups, tip of clavus, spot at base and larger one at middle of corium, broadly across apices of corium and embolium, brownish black or piceous. *Cuneus* pale, opaque, punctures chiefly concolorous, basal angle and apical half brownish black. *Membrane* practically hyaline, the anal margin and a small point at tip of smaller areole fuscous, brachium frequently infuscated.

Legs: yellowish and darkened with reddish; femora strongly reddish on apical half, an indistinct paler band before apex, the extreme tips also more yellowish; tibiae biannulate on basal half with reddish, also a spot on knee, broadly brownish at apices; tarsi yellowish brown; claws deeply cleft, arolia slender, bristle-like, erect, nearly parallel but converging slightly at apices.

Venter: reddish, shining, pale pubescent; genital claspers (fig. 39) distinctive of the species.

♀. Length 4.9 mm., width 2.65 mm.; very similar to the male in form and color; segment II, length 1.6 mm., only very slightly more slender than in the male, exserted hairs and coloration not differing from male.
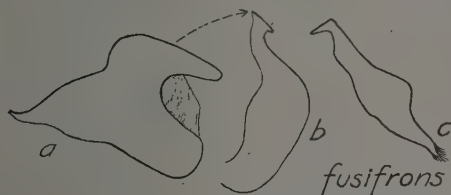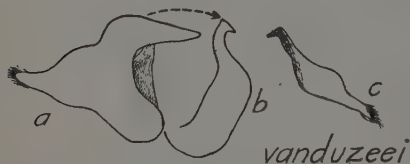

Fig. 39. *Deraeocoris vanduzeei*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Holotype: ♂ June 5, San Diego County, California (E. P. Van Duzee); collection of E. P. Van Duzee. *Allotype*: same data as the type. *Paratypes*: CALIFORNIA,—2♀ June 5, ♀ June 7, ♂ June 12, ♀ June 19, San Diego County (E. P. Van Duzee). 1♂ 1♀, Los Angeles County (Coquillett). ♀ June 9, Pasadena (Grinnell).

Deraeocoris rufiventris new species

Closely related to *vanduzeei* but larger and differently colored; dorsum rufo-piceous, cuneus reddish on the basal half, legs and ventral surface largely reddish.

♂. Length 5.3 mm. *Head*: width 1.03 mm., vertex .51 mm., length .6 mm.; structurally very similar to *vanduzeei;* yellowish to reddish, rather broadly at apex and geminate mark on basal half of tylus, bucculae, and dorsal margin of lorae, brownish to piceous. *Rostrum,* length 2.17 mm., attaining posterior margins of middle coxae, yellowish to brown, piceous toward apex.

Antennae: segment I, length .48 mm., fusco-brownish; II, 1.51 mm., gradually thickened from base toward apex, scarcely attaining the thickness of segment I, dusky pubescent, length of longest exserted hairs equal to twice greatest thickness of segment, yellowish, apical two-fifths black; III, .62 mm., yellowish, dusky at apex; IV, .45 mm., fusco-brownish.

Pronotum: length 1.22 mm., width at base 2.14 mm., anterior angles .88

mm.; collar .71 mm., opaque, brownish; disk rufo-piceous, coarsely and rather irregularly punctate, beset with numerous long erect hairs, longest at lateral margins; calli slightly convex, more nearly black than central area of pronotal disk; propleura dark reddish, piceous above, more coarsely punctate bordering the dorsal margin; xyphus convex anteriorly, reddish. *Scutellum* strongly convex as in *vanduzeei,* smooth and shining, rufo-piceous, paler at slender apex and basal angles. *Sternum* and pleura dark reddish; ostiolar peritreme reddish.

Hemelytra: width 2.74 mm., structurally nearly as in *vanduzeei;* rufo-piceous, more reddish brown between the punctures on clavus. *Cuneus* with coagulated red, apical one-third and narrowly at inner basal angle piceous, punctures concolorous. *Membrane* fuliginous, slightly paler bordering tip of cuneus, veins and apical half of areoles darker.

Legs: sanguineous to dark red, femora with an indistinct paler band on apical half; tibiae more distinctly hairy than in *vanduzeei,* triannulate with pale, broadest band at middle of apical half, the second at middle of basal half, third and narrowest band just beneath the knee; tarsi yellowish to fuscous; claws and arolia similar to those in *vanduzeei.*

rufiventris

Fig. 40. *Deraeocoris rufiventris,* male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: sanguineous to rufo-piceous, pale pubescent; genital claspers (fig. 40) distinctive but exhibiting a close relationship with *vanduzeei.*

♀. Length 5.3 mm., width 2.87 mm.; very similar to the male but slightly more robust; segment II, length 1.54 mm., only very slightly more slender than in male, yellowish, tinged with red near base, the apical one-fourth black.

Holotype: ♂ June 28, San Diego County, California (E. P. Van Duzee); collection of E. P. Van Duzee. *Allotype*: same data as the type. *Paratypes*: 7♂ 5♀, taken with the types.

Deraeocoris californicus new species

Ground color chiefly honey yellow, scutellum yellowish brown, hind tibiae with a brown annulus near middle, also a brown band on apical half of femora; pronotal disk distinctly hairy, finely and rather closely punctate.

♂. Length 6.2 mm. *Head*: width 1.08 mm., vertex .52 mm., length .65 mm.; carina obsolete, collum moderately exposed, brownish, separated from vertex by a groove; strongly pubescent or hairy, shining; testaceous, geminate mark on basal half of tylus, spot beneath front margin of eye, slender dorsal margin of lorae, reddish brown to piceous. *Rostrum,* length 2.28 mm., attaining hind margins of middle coxae, testaceous, darker apically.

Antennae: (missing in the only male specimen).

Pronotum: length 1.42 mm., width at base 2.48 mm., anterior angles 1.05

mm., collar .85 mm.; disk moderately convex, distinctly hairy, finely and rather closely punctate, lateral margins distinct, very slightly sinuate, anterior angles rounded; honey yellow or slightly brownish, punctures concolorous; calli marked with black, a line bordering hind margin, recurved slightly at outer angles and joined at middle, an arc bordering inner anterior angles, a transverse line on disk of each but frequently interrupted, sometimes extending to join with a black mark near anterior angles of pronotal disk; xyphus slightly convex anteriorly, pale pubescent. *Scutellum* convex, smooth and shining, pilose, brownish, slightly paler at basal angles and apex. *Sternum* and pleura testaceous to brownish; ostiolar peritreme pale.

Hemelytra: width 3.1 mm.; embolar margin straight along middle, rounded slightly near each end; moderately convex, heavily pubescent or hairy, rather finely punctate, punctures infuscated; testaceous or honey yellow, corium with spot at middle, smaller one at base, a broad spot at outer apical angle and slightly invading the embolium, brownish black. *Cuneus* pale, narrowly at inner basal angle and frequently the apex dark brownish, punctures concolorous. *Membrane* pale fuliginous, veins dark brown.

Legs: thickly clothed with prominent pale hairs, testaceous; femora with a dark brown mark on dorsal and anterior face near middle of apical half; hind tibiae with brownish band at middle, sometimes nearly obsolete; claws deeply cleft, arolia slender, bristle-like, erect, nearly parallel but slightly converging at apices.
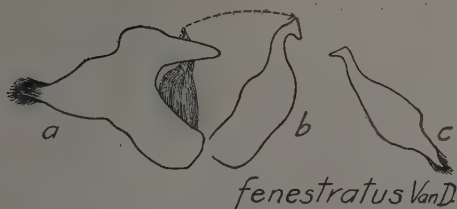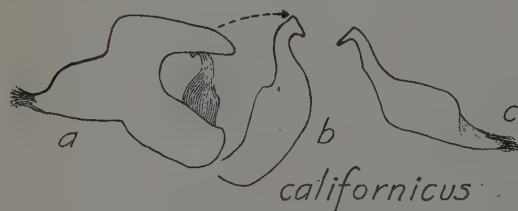

Fig. 41. *Deraeocoris californicus*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: testaceous, becoming more or less tinged with reddish, pale pubescent; genital claspers (fig. 41) distinctive of the species but exhibiting a close relationship with *cerachates*.

♀. Length 6.3 mm., width 3 mm.; very similar to the male in form and coloration but the blackish spots on hemelytra much reduced in size, frequently absent from apex of corium. *Antennae*: segment I, length .54 mm.; II, 1.68 mm., slender, slightly enlarged at apex but not attaining the thickness of segment I, clothed with erect pale hairs, length of longest hairs equal to three times greatest thickness of segment; III, .65 mm.; IV, .45 mm.; all segments yellowish, very little darker at apex of segment II.

Holotype: ♂, Los Angeles County, California (Coquillett); Cornell University collection. *Allotype*: June 8, San Diego County, California (E. P. Van Duzee). *Paratypes*: CALIFORNIA,—♀, taken with the allotype. ♀, "Los Ang." [Los Angeles] (Uhler collection).

Deraeocoris californicus desiccatus new variety

♂. Length 5.5 mm., width 2.59 mm. Structurally very similar to if not identical with the typical *californicus;* ground color pallid and more or less bleached, pronotal disk coarsely, deeply, and more sparsely punctate than in *californicus,* punctures on sub-basal margin becoming piceous; black marks on calli distinctly piceous while blackish spots on corium are nearly obsolete.

Antennae: segment I, length .45 mm.; II, 1.48 mm., gradually enlarged from base to middle, nearly cylindrical on apical half and equal to segment I in thickness, pale pubescent, length of longest exserted hairs equal to twice greatest thickness of segment, pale, becoming brownish near apex; III, .57 mm., brownish; IV, missing.

♀. Length 5.6 mm., width 2.9 mm., embolar margin more distinctly arcuate than in the typical *californicus;* more pallid than in the male, infuscations of hemelytra nearly obsolete but the piceous markings on calli equally distinct.

Holotype: ♂, September, Palo Alto, California (J. C. Bradley); Cornell University collection. *Allotypes:* taken with the type. *Paratypes:* 2♀, August, San Francisco, California (J. C. Bradley).

Deraeocoris californicus bradleyi new variety

♀. Length 5.6 mm., width 2.9 mm.; very similar in structure to the typical *californicus* but smaller, more ovate, and darker in color; frons testaceous, pronotum with punctures piceous on the sub-basal margin, calli heavily lined with black as in *desiccatus;* scutellum pale, piceous on the median line, or the median line pale and leaving a vitta each side, the vittae sometimes constricted at middle thus tending to form four piceous spots; corium broadly piceous across apex, a large spot at middle and a smaller one at base; membrane pale fuscous, paler near tip of cuneus, veins darker fuscous.

Holotype: ♀, August, San Francisco, California (J. C. Bradley); collection of E. P. Van Duzee. *Paratypes:* 2♀, taken with the type.

Deraeocoris californicus rufocuneatus new variety

♀. Length 5.7 mm., width 2.9 mm.; very similar to *bradleyi* but differs as indicated in the key; cuneus sanguineous, paler at outer margin, frons transversely marked with black each side of median line, also black bordering front margin of eye and projecting in a spur upon vertex.

Holotype: ♀ June 2, Mission Canyon, Santa Barbara, California, (Harold Morrison); author's collection.

Deraeocoris cerachates Uhler

1894 *Deraeocoris cerachates* Uhler, Proc. Calif. Acad. Sci., ser. 2, iv, p. 265.

1917 *Camptobrochys (Mycterocoris) cerachates* Van Duzee, Cat. Hemip., p. 355.

Pale yellowish to rich brownish, becoming blackish on corium and clavus, head marked with black, calli lined with piceous; pubescence moderate, not conspicuously hairy, dorsum with long hairs only at anterior angles of pronotum; erect hairs on antennae scarcely greater than twice the thickness of segment II.

♂. Length 6.7 mm. *Head*: width 1.17 mm., vertex .57 mm., length .83 mm.; carina very feeble, front moderately convex, smooth and shining; yellowish and marked with brown and black, front each side of median line, bordering inner margin of eye and projecting toward the median line on vertex, geminate mark on basal half of tylus with median spot at base, dorsal half of lorae and a spot at base of genae, brownish to black. *Rostrum*, length 2.28 mm., scarcely attaining the posterior margins of middle coxae, yellowish, becoming blackish at apex.

Antennae: segment I, length .54 mm., slightly infuscated beneath, clothed with pale hairs, the longest of which are little greater than the thickness of the segment; II, 1.65 mm., slender, slightly but gradually thickened from base (.057 mm.) to apex (.095 mm.), apical one-fourth infuscated, clothed with several erect pale hairs, the longest of which are little greater than twice thickness of segment; III, .63 mm., infuscated, fine erect hairs equal to twice the thickness of the segment; IV, .51 mm., infuscated.

Pronotum: length 1.34 mm., width at base 2.45 mm., anterior angles 1.14 mm., collar .88 mm.; disk deeply and irregularly but not densely punctate, moderately convex, lateral margins distinctly sulcate, slenderly carinate, more distinctly so on the basal half; anterior margin and angles clothed with fine pale hairs, the discal area very finely pubescent; calli convex, smooth and shining. confluent, pale between and just before, delimited behind by a heavy black line which is recurved at the outer margin, anterior inner angles broadly black, an irregular disconnected line running through the middle and curving toward a heavy black spot at the anterior angles of disk; disk yellowish to rich brown, becoming blackish on the sub-basal margin, narrow basal margin and the median line distinctly pale; propleura yellowish to brownish, the coxal margin anterior to the coxal cleft very prominent, distinctly flaring; xyphus pale, pubescent, a distinctive black spot at each anterior angle just before the coxa. *Scutellum* impunctate, shining, convex, finely pubescent; pale, black each side of the median line and becoming brown at base, mesoscutum brown. *Sternum* and pleura yellowish.

Hemelytra: width 3.1 mm.; coarsely and deeply punctate, shining, finely pale pubescent; pale, punctures of clavus and corium black, the dark color spreading to connect with adjacent punctures, apex of corium and a large irregular spot at middle blackish; embolium prominent, pale, invaded by blackish at apex, from base to apex slightly arcuated. *Cuneus* pale, black across the inner basal margin, narrow apex blackish. *Membrane* fumate, slightly darker on the apical half, paler near tip of cuneus, veins brownish.

Legs: pale to yellowish, not unusually hairy, longest hairs on femora scarcely equal to the thickness of that member, length of hairs on tibia scarcely greater than thickness of tibia; hind femora with an indistinct brown mark on anterior face just beyond middle, a faint indication of a second mark nearer the apices; tibiae becoming brownish at apices, the hind pair with an indistinct brown band at middle; tips of tarsi fuscous.

Venter: brownish, becoming piceous on sides of genital segment, the sides with a series of large piceous spots, one on each segment just beneath the spiracle; finely pale pubescent; genital claspers (fig. 42) distinctive of the species.
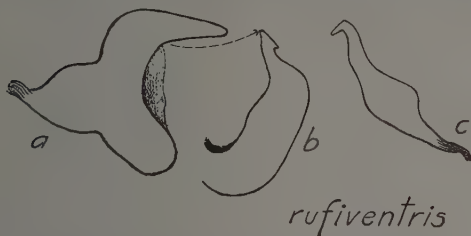

Fig. 42. *Deraeocoris cerachates*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

♀. Length 6.4 mm., width 3 mm.; very similar to the male but the black coloration much reduced, membrane nearly clear; segment II, length 1.68 mm., slender, only very slightly thickened at apex, length of exserted hairs about equal to three times thickness of segment, yellowish; sides of venter obscurely marked with a row of brown spots.

Allotype: ♂ June 9, Santa Cruz County, California, alt. 600 ft. (W. M. Giffard); collection of California Academy of Sciences.

Specimens examined: CALIFORNIA,— ♀ July 10, Clayton, Shasta County (E. P. Van Duzee). ♀ July 15, Pescadero, San Mateo County. OREGON,— ♂ June 8, Josephine County (F. W. Nunenmacher).

This species was described by Uhler from a single female specimen from San José del Cabo, Lower California, and is now preserved in the collection of the California Academy of Sciences.

The present description is drawn from a male specimen which Mr. Van Duzee has compared with the type and pronounced identical. Uhler states in the original description: "rostrum reaching over the posterior coxae." At the writer's request Mr. Van Duzee sent the following notes on the type: "The rostrum scarcely passes the apex of the intermediate coxae, it is flexed somewhat and the best one can do is to estimate. Uhler might easily have thought it would pass over the base of the hind coxae, and it might altho I would estimate it as just attaining the apex of the intermediate. The callosites are outlined in piceous."

KEY TO THE SPECIES AND VARIETIES OF GROUP VII

1. Head except tylus, pronotum, scutellum, and hemelytra except apex
    of cuneus, reddish   .   .   .   ..   *ruber ruber* Linn. p. 191
    Hemelytra or pronotum, or both, more or less blackish   .   .   .   2
2. Hemelytra reddish, pronotal disk black or largely blackish   .   .
    .   .   .   .   *ruber bicolor* n. var. p. 193
    Hemelytra and pronotum more or less blackish   3
3. Pronotal disk largely, scutellum, corium and embolium except apically,
    reddish   .   .   .   .   .   .   *ruber danicus* Fabr. p. 193

Pronotum, scutellum, hemelytra except narrowly at base of embolium
and corium, black   4

4. Cuneus reddish on the basal half   .   *ruber segusinus* Müller p. 193
   Cuneus entirely black .   .   .   .   *ruber concolor* Reut. p. 194

Deraeocoris ruber (Linnaeus)

1758 *Cimex ruber* Linnaeus, Syst. Nat., edn. 10, p. 446.
1761 *Cimex ruber* Linnaeus, Faun. Suec., p. 251.
1761 *Cimex gothicus b.* Poda, Insecta Musei Graecensis, p. 57. (not Linnaeus)
1763 *Cimex gothicus* Scopoli, Ent. Carn., p. 131. (not Linnaeus)
1764 *Cimex No. 17* Geoffroy, Hist. Abreg. des Ins., i, p. 444.
1764 *Cimex No. 5o* Geoffroy, Hist. Abreg. des Ins., i, p. 459.
1767 *Cimex ruber* Linnaeus, Syst. Nat. edn. 12, i, p. 723.
1767 *Cimex laniarius* Linnaeus, Syst. Nat., edn. 12, i, p. 726.
1775 *Cimex capillaris* Fabricius, Syst. Ent., p. 725.
1776 *Cimex cimbricus* Müller, Zool. Danicae Prodr., p. 106.
1778 *Cimex cimbricus* Goeze, Ent. Beytr., ii, p. 252.
1778 *Cimex croceus* Goeze, Ent. Beytr., ii, p. 265.
1778 *Cimex rubro-acuminatus* Goeze, Ent. Beytr., ii, 268.
1778 *Cimex luteus* Goeze, Ent. Beytr., ii, p. 278.
1778 *Cimex biguttatus* Goeze, Ent. Beytr., ii, p. 278.
1781 *Cimex capillaris* Fabricius, Species Ins., ii, p. 372.
1781 *Cimex gothicus* Schrank, Enum. Ins. Austr., p. 283. (not Linnaeus)
1781 *Cimex rubens* Harris, Expos. Eng. Ins., p. 90, pl. 26, fig. 10.
1781 *Cimex melinus* Harris, Expos. Eng. Ins., p. 90, pl. 26, fig. 11.
1785 *Cimex croceus* Geoffroy *in* Fourcroy, Ent. Paris., i, ·p. 200.
1785 *Cimex flammeus* Geoffroy *in* Fourcroy, Ent. Paris., i, p. 210.
1787 *Cimex capillaris* Fabricius, Mantissa Ins., ii, p. 305.
1788 *Cimex rufescens* Gmelin, *in* Linnaeus, Syst. Nat., edn. 13, iv, p. 2160.
1788 *Cimex fuliginosus* Gmelin, *in* Linnaeus, Syst. Nat., edn. 13, iv, p. 2164.
1788 *Cimex chrysocephalus* Gmelin, *in* Linnaeus, Syst. Nat., edn. 13, iv, p. 2164.
1788 *Cimex haematocephalus* Gmelin, *in* Linnaeus, Syst. Nat., edn. 13, iv, p. 2166.
1788 *Cimex haematostictos* Gmelin, *in* Linnaeus, Syst. Nat., edn. 13, iv, p. 2181.
1788 *Cimex adustus* Gmelin, *in* Linnaeus, Syst. Nat., edn. 13, iv, p. 2185.
1790 *Cimex gothicus* Rossi, Fauna Etrusca, ii, p. 249. (not Linnaeus)
1794 *Lygaeus eapillaris* Fabricius, Ent. Syst., iv, p. 180.
1801 *Cimex bimaculatus* Schrank, Fauna Boica, 1801, p. 88.
1801 *Cimex olivaceus* Schrank, Fauna Boica, 1801, p. 89. (not Fabricius)
1803 *Capsus capillaris* Fabricius, Syst. Rhyng., p. 244.
1804 *Capsus capillaris* Latreille, Hist. Nat. Crust. Ins., xii, p. 232.
1806 *Cimex geniculatus* Turton, Syst. Nat., ii, p. 687.
1835 *Capsus capillaris* Burmeister, Handb. d. Ent., ii, p. 274.
1840 *Phytocoris (Capsus) capillaris* Blanchard, Hist. des Ins., Hemip., p. 139.
1843 *Capsus capillaris* Amyot et Serville, Hist. Nat. Ins., Hemip., p. 281.
1852 *Capsus capillaris* Costa, Cimic. Reg. Neap., Cent., iii, p. 44.
1861 *Capsus capillaris* Fieber, Eur. Hemip., p. 266.
1865 *Capsus capillaris* Douglas and Scott, Brit. Hemip., p. 442, pl. 14, fig. 8.

1868 *Deraeocoris capillaris* Stål, Hem. Fabr., i, p. 87.
1869 *Capsus capillaris* Puton, Cat. Hem. Het., p. 23.
1871 *Capsus (Capsus) capillaris* Thomson, Opusc. Ent., iv, p. 430.
1875 *Deraeocoris laniarius* Reuter, Rev. Crit. Caps., [ii], p. 72.—Acta Soc. Faun.
        Fl. Fenn., i, p. 88.
1875 *Capsus laniarius* Puton, Cat. Hemip., edn. 2, p. 68.
1875 *Capsus laniarius* Saunders, Trans. Ent. Soc. London, 1875, p. 271.
1876 *Capsus laniarius* Reiber et Puton, Cat. Hem. Het. l'Alsace et Lorraine,
        p. 26.
1878 *Capsus capillaris* Uhler, Proc. Bost. Soc. Nat. Hist., xix, p. 408.
1886 *Capsus laniarius* Puton, Cat. Hem. Palearc., edn. 3, p. 51.
1886 *Deraeocoris capillaris* Uhler, Check List Hemip., p. 19.
1888 *Deraeocoris segusinus* Reuter, Acta Soc. Sci. Fenn., xv, p. 649, No. 254.
1890 *Deraeocoris seguisinus* Atkinson, Cat. Capsidae, p. 100.
1892 *Capsus laniarius* Saunders, Het. Brit. Isds., p. 260.
1895 *Capsus laniarius* Douglas, Ent. Mon. Mag., ser. 2, vi, p. 238.
1896 *Deraeocoris segusinus* Reuter, Hem. Gymn. Eur., v, p. 32.
1899 *Capsus ruber* Puton, Cat. Hem. Palearc., edn. 4, p. 64.
1902 *Deraeocoris segusinus* Hüeber, Jahr. ver. Nat. Württ., 1902, p. 102; (Sep.)
        Synop. deut. Blindw., i, p. 394.
1905 *Deraeocoris segusinus var. capilaris* Heidemann, Jour. N. Y. Ent. Soc.,
        xiii, p. 48.
1908 *Deraeocoris ruber* Horváth, Ann. Mus. Natl. Hung., vi, p. 5.
1909 *Deraeocoris ruber* Oshanin, Verz. Palae. Hemip., i, p. 755.
1910 *Deraeocoris seguisinus* Banks, Cat. Nearc. Hem. Het., p. 43.
1912 *Deraeocoris ruber* Oshanin, Kat. Palae. Hemip., p. 67. (as pseudotype)
1912 *Capsus seguisinus* Jensen-Haarup, Danmarks Fauna, xii, p. 233.
1917 *Deraeocoris ruber* Parshley, Occas. Papers Bost. Soc. Nat. Hist., vii, Fauna
        N. E. 14, Hem. Het., p. 93.
1917 *Deraeocoris ruber* Van Duzeé, Cat. Hemip., p. 356.
1920 *Deraeocoris ruber* J. Sahlberg, Bidrag Känn. Finl. Nat. Folk, lxxix, No.
        2, p. 128.

Deraeocoris ruber ruber (Linnaeus)

♀. Length 7.2 mm. *Head*: 1.37 mm., vertex .65 mm., length .83 mm.; tylus strongly compressed, outline of head appearing nearly triangular when viewed from above, vertex equal in width to the collum, eyes sloping forward away from collar, broadly oval when viewed from the side; vertex ecarinate, sloping backward and downward at posterior margin of eyes, collum moderately exposed, abruptly elevated above the vertex; front convex, smooth and shining, tylus prominent, facial angle equal to a right angle, lower face finely pubescent; fulvo-testaceous, tylus, dorsal margin of bucculae, small spot on vertex at dorsal margin of eye and sometimes a spot at median line of front, black. *Rostrum*, length 2.9 mm., reaching to middle of hind coxae, brownish to brownish black, paler at the joints.

Antennae: segment I, length .8 mm., reaching beyond tip of tylus by slightly more than half its length, piceous; II, 2.42 mm., slender on basal half but thickened apically, nearly attaining the thickness of segment I, the clavate

portion more thickly and closely set with short stiff black hairs, longest hairs not exceeding greatest thickness of segment, piceous, yellowish brown on the middle one-third; III, 1 mm., slender, tapering from base to more slender at apex, yellowish; IV, .54 mm., fusco-brownish.

Pronotum: length 1.74 mm., width at base 2.68 mm., anterior angles .97 mm. collar .85 mm.; disk strongly convex but more so on the basal half, deeply and rather closely but irregularly punctate, immarginate, much narrowed anteriorly, little wider than collar at anterior margin; calli small, slightly convex, subconfluent, extending to anterior margin of pronotal disk, irregularly delimited behind by coarse punctures, not differing in color from the adjoining disk; reddish yellow or fulvo-testaceous, finely pubescent, punctures becoming piceous; propleura punctate, punctures concolorous; xyphus flat, finely pubescent. *Scutellum* convex, rather sparsely and finely punctate, shining, finely pubescent, reddish yellow; mesoscutum slightly exposed, piceous. *Sternum* reddish, becoming darker each side of the median line; pleura reddish, shining, finely pubescent; ostiolar peritreme pale, sometimes tinged with yellowish.

Hemelytra: width 3.4 mm., embolar margin nearly straight along middle, rounding in to the fracture at distal end; moderately convex, nearly glabrous, shining, rather finely but closely punctate, largest punctures on clavus near scutellum, punctures concolorous, a few becoming piceous; fulvo-testaceous to reddish, outer edge of embolium, slender outer margin of corium near apex, and slender edges of the commissure, piceous. *Cuneus* sanguineous, paler at outer margin, apex black. *Membrane* infuscated, slightly paler near tip of cuneus, veins brownish black, the darker color invading the membrane slightly each side.

Legs: brownish black, apical one-fourth of femora reddish except for a blackish line on the dorsal face; tibiae yellowish to reddish, becoming infuscated at apices and on dorsal surface near base, anterior face with a row of distinct colored spines, pubescent hairs short; tarsi fusco-brownish, claws deeply cleft (fig. 2, F); arolia slender, bristle-like, erect, nearly parallel but slightly converging at the apices.
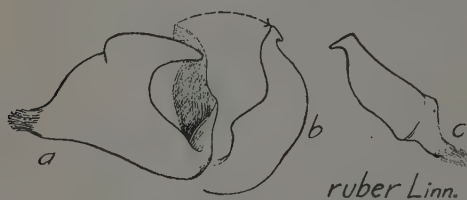
Fig. 43. *Deraeocoris ruber*, male genital claspers. a, left clasper, lateral aspect; b, internal arm of left clasper; c, right clasper, lateral aspect.

Venter: piceous, broadly reddish on the sides, finely pubescent; male genital claspers are figured from variety *segusinus*.

Plesiotype: ♀ July 14, Brooklyn, New York (Wm. T. Davis); author's collection. *Specimens examined*: CONNECTICUT,—♀ June 27, New Haven (B. H. Walden). ♀ July 9, ♀ July 21, New Haven (M. P. Zappe). NEW YORK,—♀ July 2, Maspeth, Long Island (C. E. Olsen).

Males of this variety are evidently scarce, indicating that the males tend to be darker colored than the females.

Deraeocoris ruber bicolor new variety

♂. Similar to the typical variety except that the pronotum is black; sometimes the lateral margins of the disk and the slender median line reddish.

Holotype: ♂ June 30, New Haven, Connecticut (M. P. Zappe); author's collection. *Specimens examined*: CONNECTICUT,—♂ July 1, New Haven (M. P. Zappe). ♀ June 26, Hartford (W. Marchand). NEW YORK,—♂ July 14, Brooklyn (W. T. Davis).

This variety apparently represents the pale color phase of the male. As is true in many species of Miridae, the males of *ruber* are normally darker colored than the females.

Deraeocoris ruber danicus (Fabricius)

1794 *Lygaeus danicus* Fabricius, Ent. Syst., iv, p. 181.
1800 *Lygaeus danicus* Wolff, Icones Cimic., i, p. 34, tab. 4, fig. 34.
1803 *Capsus danicus* Fabricius, Syst. Rhyng., p. 246.
1804 *Capsus danicus* Latreille, Hist. Nat. Crust. Ins. xii, p. 232.
1806 *Cimex Daniae* Turton, Syst. Nat., ii, p. 674.
1807 *Lygaeus danicus* Fallén, Monog. Cimic. Suec., p. 93.
1829 *Phytocoris danicus* Fallén, Hemip. Suec., p. 109.
1831 *Capsus danicus* Hahn, Wanz. Ins., i, p. 17, fig. 9.
1861 *Capsus capillaris var. b.* Fieber, Eur. Hemip., p. 266.
1875 *Deraeocoris laniarius var. b.* Reuter, Rev. Crit. Caps., [ii], p. 72.—Acta Soc. Faun. Fl. Fenn., i, p. 88.
1890 *Deraeocoris seguisinus* var. *danicus* Atkinson, Cat. Capsidae, p. 101.
1896 *Deraeocoris segusinus var. b. danicus* Reuter, Hem. Gymn. Eur., v, p. 33.
1909 *Deraeocoris ruber* var. *danicus* Oshanin, Verz. Palae. Hemip., i, p. 756.
1917 *Deraeocoris ruber* var. *danicus* Van Duzee, Cat. Hemip., p. 357.

♀. Head reddish, tylus and a mark extending from dorsal margin of eye to the collum, black; pronotum reddish, becoming black on the basal half but not covering the basal angles; scutellum and hemelytra reddish, clavus and rather broadly across apical end of corium blackish; cuneus red, the apical one-third black; legs and ventral surface similar to those of the typical form.

Plesiotype: ♀ July 12, New Haven, Connecticut (M. P. Zappe); author's collection. *Specimens examined*: MASSACHUSETTS,—♀ July 12, Beach Bluff; ♀ July 24, Marblehead (H. M. Parshley).

This variety represents the usual dark form of the female.

Deraeocoris ruber segusinus (Müller)

1766 *Cimex segusinus* Müller, Manip. Ins. Taur., p. 191.
1787 *Cimex tricolor* Fabricius, Mantissa Ins., ii, p. 306.
1794 *Lygaeus tricolor* Fabricius, Ent. Syst., iv, p. 181.
1800 *Lygaeus tricolor* Wolff, Icones Cimic., i, p. 35, tab. 4, fig. 35.

1803 *Capsus tricolor* Fabricius, Syst. Rhyng., p. 246.
1804 *Capsus tricolor* Panzer, Fauna Germ., fasic. xciii, fig. 20.
1804 *Capsus tricolor* Latreille, Hist. Nat. Crust. Ins., xii, p. 233.
1833 *Capsus tricolor* Dufour, Recher. Anat. Hemip., p. 176.
1835 *Capsus tricolor* Herrich-Schäeffer, Nomen. Ent., i, p. 51.
1837 *Capsus tricolor* Spinola, Essai sur les Hémip., p. 190.
1843 *Capsus tricolor* Meyer, Verz. Schw. Rhyn., p. 108.
1855 *Capsus (Deraeocoris) tricolor* Kirschbaum, Jahr. ver. Nat. Herz. Nassau,
        x, p. 212; (Sep.) Rhyn. v. Wiesb., Caps., p. 52.
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1875 *Deraeocoris laniarius var. c.* Reuter, Rev. Crit. Caps., [ii], p. 73.—Acta
        Soc. Faun. Fl. Fenn., i, p. 89.
1890 *Deraeocoris seguisinus* var. *tricolor* Atkinson, Cat. Caps., p. 101.
1896 *Deraeocoris segusinus var. c. tricolor* Reuter, Hem. Gymn. Eur., v, p. 33.
1909 *Deraeocoris ruber* var. *segusinus* Oshanin, Verz. Palae. Hemip., i, p. 756.
1917 *Deraeocoris ruber* var. *segusinus* Van Duzee, Cat. Hemip., p. 358.

♂. Black, front of head, base of corium and embolium, and basal half of cuneus, reddish; ventral surface of body black, ostiolar peritreme pale; legs colored as in the typical variety or only slightly darker.

Antennae: segment I, length .77 mm., black; II, 2.42 mm., slender on basal half, gradually thickened from middle toward apex, practically attaining the thickness of segment I, black, thickly clothed with short stiff black hairs, longest hairs scarcely attaining greatest thickness of segment; III, 1.03 mm., yellowish brown; IV, .65 mm., fusco-brownish.

Venter: black, shining, yellowish pubescent; genital claspers (fig. 43) distinctive of the species.

Plesiotype: ♂ June 29, White Plains, New York (C. E. Olsen); author's collection. *Specimens examined*: CONNECTICUT,—♂ July 21, New Haven (M. P. Zappe). MASSACHUSETTS,—♂ Aug. 16, Beach Bluff; ♂ July 24, Marblehead (H. M. Parshley). NEW YORK,—♂ June 20, ♂ July 10, Maspeth, Long Island (C. E. Olsen).

This variety represents the normal color phase of the male.

Deraeocoris ruber concolor (Reuter)

1896 *Deraeocoris segusinus var. f. concolor* Reuter, Hem. Gymn. Eur., v. p. 34.
1909 *Deraeocoris ruber* var. *concolor* Oshanin, Verz. Palae. Hemip., i, p. 756.
1917 *Deraeocoris ruber* var. *concolor* Van Duzee, Cat. Hemip., p. 358.

The writer has not seen an example of the variety *concolor* Reuter.

All the varieties of *ruber* are merely melanic color forms, but as such, varietal names are useful for separating specimens into groups having the same general aspect. Each particular color phase is an in-

dex to the conditions of environment under which the bug developed.

The distribution of *ruber* in North America would indicate that the species had been introduced from Europe through the agencies of man. Uhler (1886) recorded *ruber* as occurring in the "N. St." The oldest specimen that the writer has seen was captured by Mr. Wm. T. Davis on Staten Island, ♂ July 10, 1888, taken on red raspberry. Mr. Davis also took several specimens on roses, July 14, 1912, in Brooklyn, New York. Their presence on rose bushes could doubtless be explained by the predaceous habits of the bugs in feeding on plant lice. Puton (1876) records *ruber* as predaceous,—"detruit les pucerons." Douglas (1895) gives some observations on the manner in which *ruber* fed upon a "pale green aphid."

SPECIES WHICH HAVE BEEN DESCRIBED OR PLACED IN THE GENUS DERAEOCORIS BUT BELONG TO OTHER GENERA

Lygus robustus (Uhler)

1895 *Camptobrochis robustus* Uhler, Hemip. Colo., p. 39.
1917 *Lygus robustus* Knight, Bul. 391, N. Y. (Cornell) Agr. Exp. Sta., p. 588.
1917 *Camptobrochys robustus* Van Duzee, Cat. Hemip., p. 354.

The writer (1917) placed this species as a Lygus and in the *pratensis* group. Among the material received for study from the National Museum, the writer has found one of the type specimens, labeled in Uhler's handwriting. It agrees in all respects with the original description and opportunity is here taken to designate it as the type. *Robustus* is most closely related to *Lygus humeralis* Knight, but is slightly larger and the anterior angles of the pronotum are less prominent.

To Uhler's description the writer desires to add the following observations on the type:

Length 6.3 mm. *Head*: width 1.26 mm., vertex .48 mm., length .63 mm., height at base .74 mm.; vertex nearly flat, carina prominent but apparently formed by the perpendicular front margin of the collum; front marked with six or seven oblique or nearly transverse, subcutaneous brownish black lines each side of the median line; rostrum (apex covered with glue) apparently reaching upon the hind coxae.

Pronotum: length 1.42 mm., width at base 2.45 mm., anterior angles 1.11 mm.; calli very slightly convex, basal margins distinctly impressed beneath the level of the pronotal disk, brownish black, more nearly black along the basal and outer margins; two brownish black stripes extending from basal margin of each callus to near middle of disk, median line paler than the general coloration of disk.

robustus Uhl.

Fig. 44. *L y g u s   robustus*, male genital claspers.

Hemelytra: width 3.1 mm.; apex of marginal vein blackish, or "with black arrest at the end of the costal area" in the words of Uhler; lateral margin of corium pale translucent, the translucent area extending across base of cuneal fracture and around basal angle of cuneus to membrane; cuneus dark brown but distinctly paler along outer margin; membrane clear, or only slightly invaded with brownish from the veins, a dark mark paralleling the brachium at apex of larger areole similar to that found in *humeralis*.

Venter: olivaceo-testaceous, brownish black along basal margin of each segment but nearly

obsolete where a pale lateral stripe is formed, spiracles surrounded with pale and this in turn by blackish which occupies the basal half of each segment above the pale lateral line, the genital segment dark brownish black; genital claspers (fig. 44) distinctive of the species.

Lectotype: ♂ "Colo. 1690." [= July 10, 1894, on Grizzly Creek, Jackson County, Colorado, from *Artemisia tridentata,* alt. 9,500 ft. (C. F. Baker)]; Cat. No. 24172, U. S. N. M.

The lectotype represents the second specimen mentioned under the original description. The writer has specimens from Jemez Springs, New Mexico, which are slightly darker in color than the type but apparently not differing sufficiently even to be recognized as a color variety.

Lygus pratensis strigulatus (Walker)

1873 *Capsus strigulatus* Walker, Cat. Heterop., vi, p. 94.
1904 *Camptobrochis strigulatus* Distant, Ann. Mag. Nat. Hist., ser. 7, xiii, p. 111.
1917 *Camptobrochys strigulatus* Van Duzee, Cat. Hemip., p. 354.

In making a study of Walker's invariably miserable descriptions of Miridae, the writer was impressed by the color markings described for *Capsus strigulatus.*   It just happens that in this case the color markings will apply only to certain color forms of *Lygus pratensis,* and one very dark form in particular with which the writer became familiar during a prolonged study of Lygus. Upon reading the description the writer turned immediately to this particular variety of *pratensis* and checked over and confirmed the few distinctive marks given for *strigulatus.* In this instance we must give Walker credit for describing a form which could not very well be confused with any species other than the varieties of *Lygus pratensis.* In fact this dark variety of *pratensis* may well be retained as a color variety and on a par with *oblineatus* Say. The writer has found variety *strigulatus* in New York and Minnesota, occurring most frequently on weeds during August and September.

Distant (1904), in making a study of Walker's types, places *strigulatus* in the genus Camptobrochis but this might be expected from any worker who had not made a close study of the genera involved. Recently the writer was agreeably surprised to find among the material from the National Museum a specimen labeled *"Capsus strigulatus* Walker" in Uhler's handwriting, representing the same variety of *pratensis* which the writer had recognized as *strigulatus* Walker!

Deraeocapsus new genus

General aspect suggestive of both Deraeocoris and Capsus but distinguished as follows: claws not cleft (fig. 2, H), pseudo-arolia absent; arolia slender, bristle-like and erect, nearly parallel but slightly converging at the apices; metatarsus distinctly thickened, about equal to twice the thickness of either of the following segments, when measured from the ventral aspect equal to the combined length of segments two and three; front tibiae with four or five heavy spines on ventral surface near apex, the arrangement of spines above and below the tibial comb also distinctive (Pl. IX, G-H); segment II of antennae strongly clavate apically; dorsum either distinctly hairy or nearly glabrous. Other characters as given in the specific descriptions by Mr. Van Duzee.

Genotype: *Deraeocoris ingens* Van Duzee (Univ. Calif. Publ., Tech. Bul., 1, p. 237).

KEY TO THE SPECIES OF DERAEOCAPSUS

Legs entirely black; pronotum and legs conspicuously hairy; segment II of antennae gradually thickened from base to near apex   .   .   .
.   .   .   .   *ingens* Van D.
Femora and basal half of tibiae reddish; not conspicuously hairy, pronotum practically glabrous; segment II of antennae strongly clavate on the apical half   .   .   .   .   *fraternus* Van D.

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LIST OF THE SPECIES OF DERAEOCORIS BY GROUPS

The University of Minnesota
Agricultural Experiment Station

Spreading and Adherence of Arsenical Sprays

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SPREADING AND ADHERENCE OF ARSENICAL
SPRAYS

By WILLIAM MOORE

SUMMARY

The addition of material similar in chemical constitution to the leaf surface causes the spray mixture to form a film of liquid over the leaf.

The positive adsorption of the added material at the leaf-spray inter-face, resulting in a lowering of the interfacial tension, appears to offer the best explanation of the results.

Different types of leaves naturally require different materials. Thus organic compounds such as beechwood creosote, carvacrol, or amyl alcohol, soluble in fats and waxes and but slightly soluble in water, produce good spreading over waxy leaves, such as cabbage.

Various proteins and plant infusions give good spreading on leaves with surfaces of cellulose, even when they are strongly cutinized, as in the case of plum and citrus leaves.

Suspensions containing small-sized particles adhere better than those with larger particles.

An even distribution of the spray over the leaf tends to increase the adherence.

The leaf surface, when wet, exhibits a negative electric charge.

The common compounds of arsenic, such as lead arsenate, paris green, calcium arsenate, and others, have particles carrying negative electric charges.

Arsenic compounds of aluminum, chromium, and iron may be pre-pared so that the particles carry a positive charge.

Ferric arsenate appears the most promising and is more toxic than lead arsenate.

Field tests show that electrically positive arsenical preparations ad-here more strongly to the leaf surface than do those which are negatively charged.

Ferric oxide, or hydroxide, by adsorbing compounds of arsenic, lower their toxicity to insects.

The ratio of the amount of the arsenic compound in the body to that in the excreta is a better basis of comparing toxicity of different arsen-ical preparations than tests based on the food consumed or the time re-quired to produce death.

INTRODUCTION

The successful use of arsenical sprays for the control of various injurious insects depends upon a number of factors. The simple recommendation of paris green or lead arsenate is not sufficient, since the results will vary greatly according to the character of the plant or insect. If the plant is particularly sensitive to arsenic, care must be taken to use an arsenical material with a very low percentage of soluble arsenic. In spraying plants subjected to moist conditions resulting from frequent light rains or fogs, the stability of the arsenical preparation becomes of prime importance. Many compounds of arsenic are decomposed by the action of water and carbon dioxide.

Leaves require a spray mixture of such a character that the film produced at the time of spraying will persist and will not tend to collect in drops and roll off. This is particularly true of waxy leaves, such as those of cabbage, or strongly cutinized leaves, such as those of the citrus fruits. Such spray mixtures are not only more economical but are also of great importance in the control of insects, which, like the plum curculio, feed on isolated portions of the plant.

Not only the nature of the plant but also that of the insect must be considered. Some insects are easily destroyed by arsenical poisons, while others require large quantities to produce the desired results. When the plant to be treated is not sensitive to soluble arsenic, a resistant insect may be destroyed by the use of a compound containing a rather high percentage of free arsenious oxide, or one which readily decomposes with the liberation of soluble arsenic. In most cases, however, the use of a very stable and insoluble arsenical substance is required. Only a small percentage of such a poison is absorbed by the alimentary tract of some insects, the major portion being excreted. The excreta in such cases may be white in color owing to the presence of lead arsenate, and chemical analysis will frequently show that more than fifty per cent of the poison consumed was not absorbed. By greatly increasing the quantity of the arsenical material applied to the leaves, the death of such insects may be produced, but such an increase is not always justified from an economic standpoint. Smaller quantities of the poison may be successfully used, providing it remains on the leaves long enough for the insect to consume a killing dose. The adherence of the dried material of the spray, that is, its ability to withstand the washing effect of rain and dew, thus assumes much importance. Plants subject to the attack of an insect over a long period of time must be treated with a very adherent spray, or the treatment must be repeated several times.

The present investigation is a study of the principles governing the uniform distribution of the spray material over the plant, and the adherence of the dried particles when subjected to rain, dew, wind, and other

influences. The object of the study is general, and no effort has been made to apply the results to the control of any particular insect.

DEFINITION OF TERMS

Many attempts have been made, in the use of insecticides and fungicides, to insure even distribution of the spray over the foliage of the treated plant. In many of the papers dealing with this matter it is not clear whether the investigator is considering the spreading of the spray over the foliage or the adherence of the dry materials. Statements that the spray did not "stick" or adhere well to the plant are frequent. In some cases, from the context, it is apparent that reference is made to spreading, the drops of the spray having failed to adhere to or spread over the leaves. The term "wetting" is frequently used as a synonym of spreading. Throughout this paper the word "spreading" will be used to denote the formation or the maintenance after being formed, of a continuous film over the surface of the leaf, and "adherence" will apply to the resistance to the action of rain, dew, and wind exhibited by the spray material after it dries. The term "wetting" may be considered as the slight chemical or physical affinity between the liquid and the solid, which is one of the factors in the formation of a continuous film.

HISTORICAL CONSIDERATION OF SPREADING

One of the earliest records of the use of a material which tends to produce the spreading of a spray over the leaves is contained in the Rapport au Ministre de L' Agriculture (1885). This report deals with the treatment of the mildew of the vine, and Davis, an investigator, is reported to have used 6 kilos of glue to 800 liters of copper sulphate solution, thinking that the glue increased the efficacy of the remedy. Whether the increased value of the spray was caused by a more even spreading or by a better adherence is not mentioned. The following year, Millardet and Davis (1885) said that the addition of glue to bordeaux did not appear to be of notable advantage.

Soap or soapsuds was early used in contact sprays with tobacco and other materials in order to insure the spreading of the insecticide over the body of the insect. Altho the earliest applications of paris green were in the form of dust, the use of suspensions of paris green or london purple in water soon developed. Gillette (1890) used soapy solutions with paris green and london purple, but found that these mixtures were more injurious than a suspension containing no soap. The addition of flour at the rate of half an ounce to a gallon was tried, but this preparation also proved more injurious. The increased injury, it was thought, was due to the greater adhesiveness of the mixture. Resin in the form of a soap, sodium resinate, was successfully used without increasing the amount of injury to the foliage. Washburn (1891) used

whale oil soap, 6 pounds to 50 gallons of a paris green suspension, thereby producing an even spread of the mixture over the fruit and leaves, and apparently rendering the poison more tenacious. Galloway (1892) used soap with different fungicides to increase spreading. Swingle (1894) recommended the use of soap with bordeaux mixture. No definite quantity was specified, it was said merely that sufficient soap should be added to give a good permanent foam. This result was usually obtained by using a quantity of soap equal to one half the combined weight of the copper sulphate and lime in the bordeaux mixture. Fairchild (1894) used soap with eau celeste, obtaining excellent spreading even on leaves with a heavy cuticle, such as those of the pear. Galloway (1894) used a resin soap with bordeaux mixture, finding it just as effective in producing a continuous film on the leaf as Ivory or whale oil soap. Lowe (1896) encountered considerable difficulty in spreading a lead arsenate spray evenly over the surface of willow leaves. Glue used at the rate of 2 quarts to 45 gallons of spray gave satisfactory results.

The indefiniteness encountered in the use of soap as a spreader for various spray mixtures was shown by the analysis of various soaps by Van Slyke and Urner (1904). They showed that in the different makes of whale oil soap the water content varied from 11.15 to 54.85 per cent and the amount of actual soap from 14.90 to 59.27 per cent. The nature of the alkali present varied greatly, as did also the quantity of fatty acids and resins. Other common soaps showed a similar variation. The addition, therefore, of a definite amount of soap to a spray may or may not cause an even distribution of the material over the leaves.

Mausier (1908) studied the spreading of a number of liquids over different solids. He realized that spreading is dependent on the nature of the solid and of the liquid, but considers this difference as due to the surface tension of the liquid. A liquid which will spread over a particular solid must possess a certain definite surface tension value. If it has this value it will spread regardless of the nature of the liquid. A spray containing 30 grams of soap to 10 liters of water with either 50 grams of oil of tar or 10 grams of formaldehyde is considered as meeting the surface tension requirements of the leaf.

Vermorel and Dantony (1910) state that a body is wetted by a liquid, i.e., the liquid spreads over it when the cohesion of the molecules of the liquid, the one for the other, is less than double their adhesion for the solid. They distinguished between the surface tension of a fresh surface of a soap solution, dynamic surface tension, and the surface tension of an old surface, static surface tension, considering that there was a direct relationship between the static surface tension of a soap solution and its ability to spread over an insect. Measurements of the surface tensions, by means of a stalagmometer, of several organic compounds were made, and it was found that none possessed as low a

surface tension as a soap solution. Since no mention is made of the time allowed for the formation and breaking away of the drop from the tip of the stalagmometer, it is doubtful whether sufficient time was allowed for the concentration of the soap in the surface layer, thus insuring a true measurement of the static surface tension. In a second paper, Vermorel and Dantony (1911) take up the addition of soap to fungicides to increase their spreading, showing that the results obtained depend largely upon the method used in the preparation of the mixture. A method is mentioned for the preparation of a colloid copper soap which exhibited good spreading properties.

Parker (1911) found that the addition of 2 or 3 bars of common laundry soap to each 50 gallons of a lead arsenate spray retarded the settling out of the suspended particles. The use of soap with arsenical sprays to retard settling and to increase spreading, when tried under orchard conditions by certain growers, was frequently accompanied by an increased injury to the foliage of the sprayed plants. These results caused Tartar and Bundy (1913) to investigate the action of soap on lead arsenate. They showed by chemical analysis that the addition of different soaps had little influence on the neutral lead arsenate $Pb_3(AsO_4)_2$, but that the addition of soap to the acid lead arsenate $PbHAsO_4$, rendered soluble a considerable quantity of the arsenate. Since the acid lead arsenate is more generally used than the neutral, the addition of soap to cause spreading can not be safely recommended. Edwardes-Ker (1913) also studied the addition of soap to lead arsenate sprays, obtaining results opposed to those of Tartar and Bundy. He found that the addition of 1 per cent of soap, either home-made or commercial, did not influence the solubility of lead arsenate suspensions. Both home-made lead arsenate, formed by the reaction of lead acetate and sodium arsenate, and commercial lead arsenate were used in the experiment. No distinction is drawn between the different kinds of lead arsenate. The mixtures of lead arsenate and soap were filtered half an hour after being made up, and the arsenic in the filtrate was determined gravimetrically as magnesium pyroarsenate. Tartar and Bundy used less soap, 4.8 grams to 1,000 cubic centimeters of water, but the mixture was allowed to stand six hours before filtering. They used the iodine titration method of Gooch and Browning in the determination of the quantity of soluble arsenic. As the lead arsenate and soap would generally be mixed for periods longer than half an hour, and even after spraying would have an opportunity for chemical reactions, it appears that the results of Tartar and Bundy more nearly represent the effect of adding soap to lead arsenate sprays.

Gastine (1912) recommended the use of saponin to reduce the surface tension of spray materials and hence to insure spreading. One of its advantages is said to be that, unlike soap, it is not precipitated by acids

or metallic solutions, and will not cause injury to the plants. Saponin can therefore be added to either fungicides or insecticides without danger of any decomposition resulting. It may be used instead of soap in the formation of emulsions. Used with beechwood creosote or coal-tar creosote the surface tension of the mixture was lower than that of the pure saponin solution.

Weinmann (1912) prepared a cupric spray with calcium polysulphide and soap, finding that this combination gave a very high drop number and spread well. The drop number of the cupric spray with soap, but without the polysulphide, was much lower. The substitution of saponin in place of soap also gave inferior results.

Vermorel and Dantony (1912), continuing their investigations, concluded that the surface tension of a spray solution is not an index of its spreading power. Solutions with different surface tensions may have the same ability to spread, or the spreading power may vary according to the nature or physical state of the material to be treated. Two distinctions are made: (1) Where the liquid is able to touch the surface, when it may spread as water on a potato leaf or may collect in a drop as water on a vine (grape) leaf; (2) where the liquid rests on the surface without touching it, as in the case of a drop of water on a cabbage leaf, a film of air being interposed between the leaf and the water. A solution of sodium oleate giving a stalagmometer reading of 142 drops may spread over a cabbage leaf and fail to spread on the leaf of a vine. They believed that the surface tension of the spray influenced its spreading less than did its surface viscosity. Whereas the sodium oleate solution giving 142 drops from the stalagmometer failed to spread over the leaves of the vine, a saponin solution giving only 101 drops, and therefore apparently possessing a higher surface tension, spread readily. This difference is thought to be explained by the higher surface viscosity of the saponin solution, so that when spread in a thin film over the leaf, surface concentration rapidly took place, thus increasing the surface viscosity to such an extent that the solution was unable to collect in a drop. A gelatin solution of 1 part in 10,000 parts of water, possessing a surface tension nearly equal to water, caused spreading when applied to the leaves of a vine. Gelatin in solution was more effective than either saponin or soap and had the further advantage of being uninfluenced by either acid, neutral, or basic materials.

In this as in the preceding paper (Vermorel and Dantony, 1910), no mention is made of the speed of formation or the rate of detachment of the drops from the tip of the stalagmometer. Concentration of the materials in the surface layer reduces the surface tension, and since different materials may vary as to the time required to concentrate in the surface layer, these measurements of surface tension are not comparable. Further, if surface concentration takes place so rapidly as to cause the

film to become so viscous that it can no longer collect in a drop, a de-
cided lowering of the surface tension should be apparent in the stalag-
mometer readings. No consideration is taken of the possibility of a
concentration of the materials at the interface of leaf and spray which
would result in a lowering of the surface tension at the interface and
tend to produce spreading.

Chappaz, G., (1913) recommends the use of saponin in preparing
sprays which will spread well and considers it superior to soap. Chapaz
(1913) reviews the recent work with spreaders, discussing soap, gelatin,
glue, and saponin. He recognizes a general but not a mathematical rela-
tionship between spreading and the drop number determined by means
of a Duclaux pipette (stalagmometer). Vermorel and Dantony (1913)
recorded several methods of preparing fungicides with casein. A solu-
tion of casein is prepared by dissolving it in a solution of 100 grams of
sodium carbonate to a liter of water. Parker (1913) used from 4 to 10
pounds flour paste with lime sulphur and nicotine sulphate to each 100
gallons of liquid. The spray was used primarily for red spider and was
tried on several different plants. Altho it was an effective spreader on
many plants, it failed when used on carnations, sweet peas, and green-
house roses. The possibility of its use as a "sticker" for lead arsenate
suspensions was considered. Glue and miscible oil mixed with lime sul-
phur was used for the control of red spider by Jones (1913). Excellent
spreading was reported on all parts of plum and peach trees and it is be-
lieved that similar results would be obtained on citrus trees. Neüls
(1913) confirmed the results of Parker (1913) on the spreading prop-
erties of lime sulphur and flour paste and the value of this spray for the
destruction of red spider.

Lafforgue (1913) points out that spreading and adherence are two
entirely different phenomena. The addition of saponin to the spray
mixture gives good spreading but not good adherence, while gelatine
spreads well and also improves the adherence.

Lefroy (1913), working in India, had determinations made of the
surface tension of the solutions used for controlling psylla attacking in-
digo. Soap solutions showed a very much lower surface tension than
water, but soap emulsions of oil or creosote exhibited a higher surface
tension than the soap solution alone. These results are opposed to the
work of Gastine (1912), who found that a saponin emulsion of beech-
wood creosote or coal-tar creosote possessed a lower surface tension than
the saponin solution. However, since no mention is made by Lefroy of
the method employed in determining the surface tension, and in view of
the fact that in one case soap and in the other saponin was used to emul-
sify the creosote, no conclusion can be reached as to the accuracy of the
results.

Astruc (1913) divides spreaders into four types: (1) Soaps; (2) saponins; (3) albuminous substances, such as albumin, gelatin, milk, dried blood, and casein; (4) organic salts of more or less limited production. No mention is made as to the nature of these organic salts. Issleib (1914) extracted 2 kilograms of "carrangeen," or pearl moss with 100 kilograms of water. The extract, a thick slimy liquid, when sprayed over the leaves formed a thick continuous coating which on drying cracked and scaled off, carrying with it the larvae or eggs of insects infesting the plant. These results are comparable to those recorded by Parker (1913), using flour paste, and no doubt this preparation would give similar spreading.

Del Guercio (1914), in Italy, recommended the use of 1 to 2 per cent of flour paste, fish glue, or other colloidal substance, with potassium or calcium polysulphide to give an even distribution of the spray over citrus trees to control *Chrysomphalus dictyospermi* var. *pinnulifera.* Rye flour is preferred, but spoiled wheat flour or the flour of other grains may be used. An even distribution was obtained regardless of the degree of maturity or the position of the treated portions. Arnal (1914) mentions that "soluble caseins," for use with bordeaux mixture, are being manufactured in France and put on the market. It may be that these preparations are similar to the casein glue being sold in the United States.

Vermorel and Dantony (1915) prepared rapidly a calcium caseinate by stirring a liter of milk of lime into a suspension of 100 grams of casein powder in a liter of water. The milk of lime may contain from 50 to 200 grams of lime without influencing the results. One liter of this solution is added to a hectoliter of alkaline bordeaux mixture to give spreading and adherence.

The most important paper, following the papers of Vermorel and Dantony, dealing with the spreading of sprays, is that of Lefroy (1915). The fact that spreading depends not only upon the value of the surface tension of the spray, but also upon the surface tension of the leaf[2] and the surface tension at the interface of the spray and the leaf, is presented by Lefroy for the first time in entomological literature. Unfortunately Lefroy becomes confused in his terms, and draws the incorrect conclusion that if the surface tension at the interface between the spray and the leaf is greater than the sum of the surface tension of the spray and that of the leaf, spreading will occur. Realizing that the surface tension of the leaf and the surface tension at the interface of leaf and spray can not be readily determined, he recommends the determination of the surface tension of the spray, which should be as low as possible. Using the term "wetting" to denote the specific attraction

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[2] Solids are usually considered as possessing a surface tension altho it has not been demonstrated.

or slight chemical affinity existing between the spray and the leaf, the statement is made that "spreading of a liquid over a surface it never wets" may occur. This conclusion does not appear to be justifiable, since if no wetting occurred the surface tension at the interface would be so high that spreading would be impossible. The theory of spreading of both sprays and dips is presented in a very interesting paper by Cooper and Nuttall (1915). First pointing out the value of having sprays and dips which will spread over the treated plant or animal, they give the principles of spreading established by Quincke (1877). Quincke studied the capillary rise of liquids in tubes of different materials, the spreading of one liquid over another liquid or a solid, and the angles formed by the liquid at its point of contact. From this study he formulated the conditions necessary for spreading to occur. These conditions in terms of sprays may be expressed by the statement that if the surface tension of the solid (leaf) is greater than the sum of the surface tension of the spray and the surface tension at the interface of spray and solid, spreading will occur. Cooper and Nuttall believe that in general this statement holds, but believe that there may be certain exceptions. Two factors are thought to be able to upset entirely this relationship. The first of these is the solvent action of the liquid on the solid, particularly in those cases where the solid is coated with wax or grease. This solvent action of the spray is believed to be independent of the surface tension at the interface of solid and liquid, but as will be shown later in this paper the solvent action of one liquid on another liquid or a solid, results in the lowering of the surface tension at the interface. Sprays, therefore, which spread because of their solvent action, are not exceptions but actually fulfil the surface tension conditions necessary for spreading to occur.

The second factor considered as vitiating the surface tension equation is the phenomenon of surface concentration. The experiments of Vermorel and Dantony are cited as showing that a spray with a high surface tension spreads well owing to its high surface viscosity resulting from a rapid surface concentration of the solute.

Since these experiments have already been discussed and will be taken up later they will not be considered further here, tho it may be said that in the opinion of the writer, they do not invalidate the surface tension relations already expressed.

Having presented the problem, Cooper and Nuttall take up the possibility of measuring the spreading power of dips and sprays. The work of Vermorel and Dantony is thought to show that the measurement of surface tension alone is insufficient to determine the spreading qualities of the liquid. The ability of the spray to produce a foam, since it depends upon surface tension and does not express the surface tension at the interface of the liquid and solid, can not be used as an index to

spreading. The weight of the quantity of liquid adhering to a solid dipped into it is largely influenced by viscosity, and is therefore not considered an accurate method of determining spreading. Spreading may be conveniently expressed by the formula $\delta s > \delta l + \delta ls$ where "δ" represents surface tension; "s", solid; "l", liquid; and "ls", the liquid-solid interface. Then $\delta s - (\delta l + \delta ls) =$ the spreading power of the liquid expressed in dynes. Cooper and Nuttall, being chiefly interested in dips where the solid is represented by the skin of the animal, usually oily in character, adopted castor oil or liquid vaseline as a liquid substitute for the solid. This substitution simplified the problem, as the surface tension of the oil and of the liquid (dip) could easily be measured and expressed in dynes. Using a modification of the drop pipette method for determining the emulsifying action of soap solutions, they measured the surface tension at the interface of the oil and the dip. Substituting the values of the different surface tensions in the above formula, a definite value for spreading, expressed in dynes, was obtained. It is pointed out, however, that this method is applicable only to soap solutions and will not give results with gelatine, saponin, or similar solutions.

This method, based on the use of an oil as a substitute for the solid, may be used only when the solid is oily or greasy, and can not be used to determine the spreading power of sprays on leaves which possess an entirely different surface.

From the results of their experiments they conclude that for comparative values the interfacial tension alone may be considered. Since this is inversely proportional to the number of drops produced by a given volume of the oil, and since the spreading varies inversely as the interfacial tension, it is directly proportional to the drop number. This conclusion, however, is based on the assumption that the liquid has a low surface tension, which, altho correct in the case of soap solutions, is not always true of spray materials which will spread. Of the two surface tensions, they consider the surface tension of the solid-liquid interface more important.

A new material and one well adapted for use in certain countries was suggested by High (1915). Fifteen pounds of cactus leaves sliced and soaked in 50 gallons of water over night is recommended as a spreader. Cactus extract gave excellent results when used with zinc arsenite, and paris green and lime, but with lead arsenate the results were unfavorable, owing to the formation of a precipitate. Cactus grown near water contains a lower percentage of the desired material and hence larger quantities were required to give the desired results.

Smith, L. B. (1916), using the method of finding the surface tension at the liquid-solid interface suggested by Cooper and Nuttall, determined the spreading power of various combinations of fish oil soap

and nicotine sulphate. No effort was made to determine the surface tension of either the oil or the spray. The sprays were tested with *Acyrthosiphum pisi* Kalt. on garden peas, *Myzus persicae* Sulz. on spinach, and *Tetranychus sp.* on strawberries. The maximum killing was reached with certain concentrations of soap or soap and nicotine sulphate. Further additions of soap failed to increase the efficacy of the spray. Using a fixed concentration of soap and increasing the concentration of nicotine sulphate reduced the spreading and also the killing power of the spray. This result was undoubtedly due to the reaction between nicotine sulphate and soap.

Lees (1917) tested the spreading of paraffin (kerosene) emulsion on cloth surfaces previously painted with boiled linseed oil and dried. A drop of the emulsion was rolled about on this surface and arbitrary values from one to three were used to express the degree of spreading of the kerosene and similar values for the aqueous phase. Based upon these preliminary tests, further experiments were made on the spreading of water solutions of gelatin, casein, soap, and paraffin emulsions on the leaves of gooseberry and sea kale and on goosebrry mildew. All the preparations gave complete spreading on gooseberry leaves bu. only certain of the emulsions gave complete spreading on kale leaves and gooseberry mildew. No attempt is made to explain the results.

Altho not directly bearing on the spreading of sprays on foliage, the experiments of Gray (1918) in preparing "wettable" sulphurs are of interest. An ounce and a half of powdered glue dissolved in 3 gallons of water thoroly wets, or spreads over, powdered sulphur, thus making possible the formation of a suspension.

Lovett (1918) studied spreaders for arsenate sprays. Spreading is thought to be caused largely by surface tension and specific gravity. It is stated that the ability of the liquid to hold the arsenate in suspension is a very fair indication of its ability to spread. This is not always true, for altho some spreaders which increase the viscosity of the medium also reduce the rate at which the suspended particles settle, this characteristic in itself can not be considered an index of spreading. Soap, glycerine, glue, casein, and an infusion of sage were tes'ed as to spreading ability and also as to the degree of injury they produced on bean foliage. An infusion of sage made by steeping *Artemesia tridentata,* Nutt. for twelve hours gave very encouraging results. The oils and other ingredients present in the infusion were no: determined but were considered as probably similar to those found in *Artemesia frigida,* Willd. by Robak (1906). This species was shown to contain an essential oil composed primarily of borneol camphor and cineol. From 4 to 8 ounces of casein converted into calcium caseinate and added to each 100 gallons of spray gave good 'spreading.

Stearns (1920) experimented with the "Irish" moss which is similar to that used by Issleib (1914), as a spreader of arsenical substances over peach foliage. Issleib's proportion of 4 pounds to 20 gallons was found to be too thick for spraying purposes, but when used at the rate of 4 pounds to 50 gallons gave good results. Calcium caseinate at the rate of 1 pound to 50 gallons also gave good results on peach foliage.

The most recent paper dealing with spreaders is that of Lovett (1920). In discussing the suspension test as an index of spreading, he says that altho not a definite criterion of spreading it "does indicate a physical quality in the solution much to be desired in a spreader." His belief that increased viscosity is accompanied by increased spreading is shown in the experiments where phosphates and sulphates are added to aqueous solutions of glue and of calcium caseinate to increase the viscosity and therefore the spreading. Increased spreading was not ob'ained.

A number of different materials were tested, not only colloids such as saponin, sage tea, gelatin, glue, calcium caseinate, corn, potato, wheat, arrowroot, and starch, but also inorganic substances such as aluminum sulphate with lime, kaolin, barium sulphate with lime, chromium fluoride with lime, calcium chromate with lime, and lead chromate with lime. None of the inorganic materials gave the desired results. On the basis of compatability, efficacy, availability, cost, and ease of preparation, he arranges the colloids in the following order of merit : Calcium caseinate, glue, gelatin, soap bark (saponin), and oil emulsion.

A new method for testing spreading in the laboratory is presented. Tubes lined with a coating of wax obtained from the surface of Ben Davis apples were used to determine the capillary rise of the different solutions. The numerical value of 3.5 (probably millimeters) is given for water, while 2 per cent gelatin had a value of 11.8, 2 per cent soap bark 2 8, 2 per cent caseinate 10.11, and 2 per cent glue 7.8. Lovett believes that the height to which the liquid rises in the capillary tube is a measure of spreading power. This is not strictly true, as only those liquids which will spread over or "wet" the surface of the tube (in this case the wax of the apple) will rise in it, and the height to which they rise is determined by the surface tension of the liquid and the angle of contact of the liquid to the wall of the tube. The use of a capillary tube will merely show whether the liquid will or will not spread. If it rises at all, spreading will occur ; and if no spreading will occur there will be no rise.

Summarizing briefly the work of the various investigators, it is apparent that various colloidal substances, such as casein, gelatin, flour, glue, and soaps modify the spray mixture to such an extent that it will remain spread out over the leaf surface in the form of a film. The surface tension relationships of the leaf and spray offer the best explanation, but in certain cases other factors are thought to influence the

results. These various colloidal substances have given good spreading on leaves with a thin cellulose epidermis, and even on leaves more or less strongly cutinized, such as those of apple, peach, grape, pear, and the citrus fruits. Results on waxy surfaces, such as the waxy bloom on the fruit of apple or plum and the leaves of cabbage, have not been attained except by the use of soap or soap emulsions. Soap will produce spreading on such surfaces, but owing to the reaction between the soap and the arsenical materials, its use may result in injury to the foliage. Other disadvantages of the use of soap are its varying composition, its reaction with hard water, and the difficulty of dissolving it without the use of heat. The following experiments were therefore undertaken to find a new material for use on waxy surfaces, and to obtain a better understanding of the causes governing spreading.

THE THEORY OF SPREADING

The manner in which surface tension is related to spreading is shown by the following illustration. Upon a liquid, B, with a surface exactly two square centimeters in area, place a drop of an immiscible liquid, A, so that its area is exactly one square centimeter. The area of the surfaces of A, B, and the surface at the interface AB is then exactly one square centimeter in each case, and the surface tension of the entire system is expressed by the equation $\delta\,A + \delta\,B + \delta\,AB$, in which δ represents the surface tension. Now assume that A is spread out until it completely covers B, then the area of the surface of A and the surface at the interface AB is in each case two square centimeters, while B no longer has an exposed surface. The surface tension of the system then becomes $2\,\delta\,A + 2\,\delta\,AB$. Subtracting the second equation from the first gives the equation $\delta\,B - \delta\,A - \delta\,AB$ as the difference between the surface tensions of the system under the two conditions. Since a system will always arrange itself so as to reduce its surface tension, if the surface tension of the system in the second state is less than in the first case, spreading will occur and the equation will be positive. If the surface tension under the original arrangement is the lowest, then the equation is negative and spreading will not occur. The surface tension conditions favorable to spreading may then be represented by the equation $\delta\,B > \delta\,A + \delta\,AB$, while conditions unfavorable to spreading may be expressed by the equation $\delta\,B < \delta\,A + \delta\,AB$. An excellent example of these conditions is the system benzene and water. A drop of pure benzene placed on the surface of pure water immediately spreads out, forming a thin film[3].

$$\delta\,H_2O > \delta\,C_6H_6 + \delta\,(H_2O-C_6H_6).$$
$$\delta = 72.05 > \delta = 28.17 + \delta = 34.68.$$

[3] The surface tension values given are those of Harkins, Brown, and Davies (1917).

In a few minutes the water becomes saturated with benzene and the benzene becomes saturated with water. The surface tension of each is lowered, while the surface tension at the interface is increased. The value for the equation becoming:

$$\text{ŏ Sat. } H_2O < \text{ŏ sat. } C_6H_6 + \text{ŏ } (H_2O—C_6H_6).$$

$$\text{ŏ} = 60.19 < \text{ŏ} = 27.90 + \text{ŏ} = 44.68.$$

The benzene which had previously been spread out in a thin film now collects in the form of a drop. In this case, at least, there is no doubt that spreading or lack of spreading may be explained on the basis of surface tension.

Unfortunately it is at present impossible to measure the surface tension of a solid, or even to prove conclusively that a solid possesses surface tension. Since the surface tension of a liquid increases as the temperature is lowered, even to the freezing point, it does not appear reasonable that surface tension completely disappears in the solid. It seems more reasonable to believe that a solid has a high surface tension which can not be demonstrated because of the immobility of the molecules. The surface tension at the interface of the solid and liquid is also impossible of measurement. With two of the surface tensions unknown, it is useless to measure the surface tension of the spray liquid, and it becomes necessary to find some other method of solving the problem.

From a consideration of the above formula, it appears that spreading can be obtained only by lowering the surface tension of the liquid or the surface tension at the liquid-solid interface, since the surface tension of the solid (leaf) can not be increased. The problem, therefore, resolves itself into this: How may the surface tension of the spray and the surface tension at the spray-leaf interface be lowered? It is well known (Willows and Hatschek, 1915) that the adsorption of a solute in the surface layer will result in the lowering of the surface tension, while if it is negatively adsorbed, the surface tension will be increased. Thus soap or saponin dissolved in water is adsorbed or collects at the surface and the surface tension lowered. Sodium chloride dissolved in water concentrates in the interior of the liquid and is therefore negatively adsorbed and the surface tension is increased. In a similar manner a dissolved substance adsorbed in the surface at the interface of the liquid and solid will lower the surface tension at this interface. The next question then is to determine what substances will be positively adsorbed in the liquid-air surface and the liquid-solid surface.

Data on this problem have been given in three different papers which are too long to be completely reviewed here. Altho the papers deal with a different problem, certain facts given in them may be directly applied to the present problem. Harkins, Brown, and Davies (1917), considering the work done when water and some other liquid come

together to form an interface, have shown that at the interface of the two liquids the molecules in the surface of the liquid orient themselves so that the active group is in contact with the water. The decrease in the free energy, i.e., the surface tension at the interface, when the surface of a second liquid approaches that of water, depends primarily on the most active group present in the molecules and secondarily on the shape and size of the molecules. The solubility in water is related to this decrease in free energy which more or less perfectly measures the attraction of the active group for the water molecule. The presence of such active groups as $COOH$, CO, CN, OH, or $CONH_2$ is sufficient to make the molecule of an organic substance soluble in water, providing the active group does not have to pull into the solution a slightly less active group, which is too long or too large.

In a second paper Harkins, Davies, and Clark (1917) show that in the surface of a liquid the molecules are so oriented that the least active group is toward the vapor phase, that is, the vapor above the liquid. At any surface or interface, the orientation of the molecules is such as to make the transition to the adjacent phase—that is, the vapor, liquid, or solid in contact with it—least abrupt. At the interface of two liquids their like parts come together in conformity with the above law. In two liquids, A and B, the portion of the molecules of A like B turn toward B and those of B like A turn toward A. If a solute is present in either of the liquids, A or B, which collects at the interface, the molecules of the solute will so arrange themselves that the parts of the molecules which are like A will turn toward A, while those like B will be attracted to B. In such a case the free surface energy, that is, the surface tension at the interface, will be reduced. An aqueous solution of a solute which is active like water but to a lesser degree, will be positively adsorbed in the surface and the least active portion will be turned toward the outside.

The third paper by Langmuir (1917) approaches the problem from a slightly different angle. Studying the spreading of oleic acid on water, the conclusion is reached that the active carboxyl groups are actually dissolved in the water but the long hydrocarbon chains have too much attraction for each other to be dissolved, hence the acid spreads out into a thin film. Oils without this carboxyl group should not spread, and in fact pure paraffin oil, which lacks an active group, fails to spread at all. Results show that the spreading of films on surfaces is determined by the shape of the molecules and by the relative activities of the different portions of the molecule. In a similar manner a substance, such as a soluble fatty acid, dissolved in water, is adsorbed in the surface layer and lowers the surface tension. Adsorption of a liquid on a solid is considered as similar to the spreading of oil on water, i.e., the portion

of the liquid similar to the solid is attracted by the molecules of the solid forming a molecular layer upon it.

Considering the data presented in these papers, the investigation became a search for those substances which possess an active group to render them soluble in water and an inactive group which will cause their adsorption in the surface layer. If the inactive group should be similar to the surface of the leaf or soluble in it, then adsorption at the spray-leaf interface would occur and would result in a lowering of the interfacial tension. A substance fulfilling one or the other of these conditions, preferably the latter, should cause spreading.

SPRAYS THAT WILL SPREAD ON CABBAGE LEAVES

An effort was made by the author in the earlier experiments to determine whether a given solution would spread or not, by means of capillarity. Altho this method might be used in considering waxy surfaces, it could not be adapted to the study of leaves with a thick cuticle. To obtain comparable results, nothing but a capillary tube possessing walls exactly similar to the leaf surface would suffice. Tests in all the experiments were therefore made by spraying the solution on the surface of the leaf by means of an atomizer.

The first efforts were directed toward producing spreading of the spray on cabbage leaves. A saturated solution in water of several organic compounds was tested. Solutions of kerosene, methyl salicylate, benzaldehyde, chloroform, camphor, and salicylic acid failed to give the desired results. Amyl alcohol and benzyl alcohol gave good results but were too expensive for actual use. Crude phenol produced spreading but since a 1 per cent solution of pure phenol failed, the results with crude phenol must have been due to impurities. Phenol possesses an active OH group, while resorcinol possesses two such OH groups. A 1 per cent solution of resorcinol failed to give spreading. It appeared therefore necessary to introduce such groups in the phenol as would decrease its solubility in water and increase its solubility in the wax of the cabbage leaf, thereby increasing its adsorption at the leaf-spray interface and lowering the interfacial surface tension. A saturated solution of beechwood creosote consisting of a mixture of cresols, $C_6H_4(OH)CH_3$, and guaiacol, $C_6H_4(OH)OCH_3$, gave excellent results. So concentrated a solution of beechwood creosote is not necessary, since a good spreading accompanied the use of a one-third and even a one-fourth per cent solution. One-fourth per cent is about the lower limit and one-third is a safer proportion. A saturated solution of carvacrol, $C_6H_3(OH(CH_3)C_3H_7)$, containing about one-twelfth of 1 per cent, and a saturated solution of eugenol, $C_6H_3(OH)(OCH_3)CH_2 \cdot CH : CH_2$, containing only about one-fifteenth to one-twentieth of 1 per

cent, gave good spreading, each being less soluble in the water and more soluble in the wax of the leaf.[4]

Most of these substances are adsorbed in the surface layer and reduce the surface tension of the solution. The question naturally arises whether the spreading is not caused by the lowering of the surface tension of the liquid itself rather than the lowering of the surface tension at the interface of the leaf and the solution. Surface tension determinations were therefore made by means of a stalagmometer. Harkins and Brown (1918), in studying this method of determining surface tension, pointed out that if the formation of the drop is too rapid, some of the liquid streaming from the tube seems to force its way into the falling drop during the time of detachment, hence increasing its weight. From the figures given, this error is not very large and can be ignored in these relative determinations. It is also stated that when dilute aqueous solutions of long chain organic molecules are used, it is often necessary for the drop to hang for half an hour to obtain the value of the static surface tension. In spraying it is really the surface tension of the solution at the moment it is sprayed over the leaf that is desired, hence a determinatin of dynamic surface tension is more important than static surface tension.

A one-third per cent solution of creosote allowed to drop at the rate of one drop per minute showed a surface tension of 49.27 dynes. One-fourth of a pound of sodium oleate to 100 gallons of water possessed a surface tension of 42.42 dynes. The soap solution, altho it possessed a lower surface tension than the creosote solution, failed to spread over cabbage leaves. A soap solution with a surface tension of 24.28 dynes gave spreading. It is therefore apparent that the spreading of the creosote solution is not owing to its low surface tension but to the lowering of the surface tension at the leaf-solution interface. Further confirmation of this statement is found in the fact that none of these solutions would spread over the leaves of citrus, guava, or other plants possessing strongly cutinized leaves but lacking the waxy surfaces.

The possibility that the results of Lovett (1918) with sage infusions may have been due to some organic principle in the essential oil of the sage, at once suggested itself. Robak (1912) has shown that another species of sage possessed an oil rich in cineol, hence a saturated solution of cineol was tried and gave good results. Since this experiment was conducted, Lovett (1920) has stated that sage infusions did not spread well over the waxy surface of apples, hence his results may have been due to some other ingredient of the infusion.

[4] A saturated solution of a mixture of xylenols sold under the name of cresylic acid (straw-colored) by the Barrett Co. will cause spreading on cabbage leaves.

No doubt a very large number of organic compounds will give similar results. Apparently all that is needed is a chemical containing an active group to make it slightly soluble in the water, and an inactive portion soluble in wax. With this principle as a base, it should be a simple matter to select the compound best suited for each particular set of conditions. The practical application of these results has been left for future investigation.

SPRAYS THAT WILL SPREAD ON OTHER LEAVES

It has been stated that these organic solutions failed to spread on leaves which did not possess a waxy coating. Other investigators have obtained good spreading on such leaves by means of various colloids, such as soap, casein, glue, and gelatin. Sodium oleate, 2 pounds to 100 gallons, gave spreading on citrus leaves, while a smaller quantity failed. Commercial casein was dissolved in water containing a very small quantity of sodium hydroxide (2 ounces to 5 pounds of casein). Such a solution containing only one-fourth pound of casein to 100 gallons of water gave very good spreading on citrus leaves, but failed on cabbage unless applied with such force that the liquid penetrated between the wax particles, reaching the epidermis below. Gelatin used at the same rate also gave favorable results on citrus leaves. Acidifying the solution did not destroy its spreading properties.

Flour paste has often been used as a spreader, but much of the protein in the flour is insoluble in water and is therefore not utilized. If about one ounce of sodium hydroxide is added to 5 pounds of flour when the paste is being prepared, all of it goes into solution. Prepared in this way, one-fourth pound of flour to each 100 gallons of the spray produces a film when sprayed over citrus leaves.

Saponin gives good results but is too expensive for general use. Jacobson (1919) has shown that alfalfa hay contains a saponin quite soluble in water. About one per cent of pure saponin was recovered from air-dried alfalfa. Alfalfa hay should therefore serve as a spreader. One hundred grams of hay was heated in 3 liters of water and allowed to stand twenty-four hours. Two and a half liters were recovered on straining. This solution was diluted until it represented only six-tenths of 1 per cent of alfalfa hay, and at this dilution gave good spreading. Five pounds of dry alfalfa would be sufficient for 100 gallons of the spray.

The question arose as to whether these results were due to the lowering of the surface tension of the liquid, to the increased surface viscosity suggested by the work of Vermorel and Dantony, or to a concentration of the materials at the leaf-spray interface, resulting in a lowering of the interfacial tension as suggested by the experiments with waxy leaves. A creosote solution with a surface tension of 49.27 dynes

failed to spread, as did also a soap solution of 38.36 dynes, while one with a surface tension of 24.28 dynes gave good spreading. A solution of gelatin of 1 part in 10,000 which will produce spreading had a surface tension of 72 dynes. Casein in solution, alkaline to litmus, had a surface tension of 64.4 dynes, while when acid to litmus the surface tension was lowered to 57.74 dynes. These values were obtained by allowing one minute for the drop to fall from the tip of the stalagmometer, and therefore represent the dynamic rather than the static surface tension. Since the spreading occurs on the leaf at once, it is apparent that the results are not due to a low surface tension.

Vermorel and Dantony (1912) explained similar results on the basis of a very rapid surface concentration of the colloid resulting in an increase in the surface viscosity so great that the film was prevented from collecting in a drop. If such a rapid concentration occurred, it should make itself manifest by its influence on the surface tension. The number of drops produced from a given volume of liquid when measured by allowing one second for each drop, compared with the number obtained when one minute was allowed, should be a fair test of the rapidity of the surface concentration which might occur on the leaf surface quickly enough to make the surface so viscous that the film could not collect in drops. Water measured at the rate of one drop per second gave 45.5 drops while at the rate of one drop per minute 46 drops were produced. Gelatin, 1 part in 10,000, gave 46 and 46.5 drops; while casein, 3 parts to 10,000, gave 46 and 52 drops when alkaline to litmus and 50 and 58 drops when acid to litmus. This increase does not appear sufficient to produce as high a surface viscosity as Vermorel and Dantony considered possible. Harkins and Brown (1918) found that the surface concentration is so slow in such solutions that a half hour must be allowed each drop to insure the maximum surface concentration and a true measurement of the static surface tension. Further, if the spreading is due to surface viscosity it should be possible to produce the film on any surface, but this can not be accomplished.

Like material has been shown to attract like, and there is a strong similarity between the colloids used and the cellulose and cutin of the leaf surface. This similarity should cause a concentration in the surface at the interface of the leaf and spray, thus reducing the interfacial tension. On the cabbage leaf the contact is with the wax, different in character from the proteins, and spreading is not obtained. Only when the spray is delivered with sufficient force to drive the liquid between the wax particles and bring it into contact with the epidermis will results be obtained.

CONCLUSION REGARDING THE PHENOMENON OF SPREADING

On the basis that substances of like nature attract each o her, materials were selected which, while soluble in water, would be attracted to the leaf surface and concentrate in the leaf-spray interface. Using materials similar in character to the wax of the cabbage leaf produced spreading but failed with leaves which did not possess the waxy coating. Protein and similar materials produced spreading on leaves with a surface of cellulose or cutin but failed to give good spreading on waxy leaves. It appears possible that an infusion of nearly any plant would serve to give spreading to a spray for use on wax-free leaves, but this statement requires confirmation.

The viscosity of some of the sprays was increased, but in the case of carvacrol, beechwood creosote, and eugenol it was not materially altered. Viscosity, therefore, is not related to spreading. Surface concentration appears not to take place rapidly enough to increase the surface viscosity to such an extent as to prevent the film from collecting into drops. The surface tension of the leaf was not altered and the values for the surface tension of the liquids did not agree with the results obtained in spreading. The reduction of the interfacial tension appears to be the most reasonable explanation of the facts. Unfortunately this surface tension has not yet been measured, nor has the concentration of the material at the leaf-spray interface been demonstrated. However, with this theory as a basis, sprays that will spread on the different types of leaves may be produced.

HISTORICAL CONSIDERATION OF ADHERENCE
THE USE OF ORGANIC MATERIALS WITH FUNGICIDES

The adherence of spray materials was studied very early in the history of spraying. In one of the earliest papers, Millardet and Davis (1886) drew attention to the fact that cupric steatite powder possesses remarkable adherence, owing to its extreme fineness. When it was demonstrated that plant diseases might be controlled by means of copper compounds, an effort was made to form on the leaf a coating of copper which would adhere well and serve as a barrier to the fungus. Crouzet (1899) recommended copper caseinate, prepared by adding raw milk to a solution of copper sulphate, as a very adherent spray. Galloway (1891) used molasses and also glue to give adherence to a mixture of copper sulphate and sodium carbonate. In the experiments of Girard (1892), molasses actually diminished the adherence of bordeaux mixture. Lavergne (1896) tested a "tannocuprique" spray, possibly copper tannate, bordeaux and sugar, and bordeaux mixture

alone, for the control of black rot. Bordeaux mixture applied six days earlier than the other- sprays gave the most satisfactory results. Cazeneuve (1898) published a paper on albuminous bordeaux mixtures, the original of which is not available. Bourcart (1913) mentioned the use by Cazeneuve of three types of albuminous bordeaux, one containing milk, one made with dried egg white, and one with dried blood. The bordeaux casein did not adhere better than bordeaux and sugar, but the other two types persisted on the foliage throughout the season. Bourcart cited only the name, hence it is not certain that he is referring to Cazeneuve (1898). Guillon and Guirand (1898) tested the adherence of different preparations to glass slides. They showed that the adherence of bordeaux mixture decreased with its age. The addition of 1 per cent molasses or three-tenths per cent gelatin increased adherence, while larger quantities decreased it. They also used 3 per cent soap with 2 per cent copper sulphate, a combination which must have resulted in the formation of a colloidal copper soap. In a second paper published the same year they give results of studies on the adherence of these materials to grape leaves. Bordeaux mixture with 2 per cent soap showed the greatest adherence, while gelatin or molasses gave poor results. Perraud (1898) studied the adherence to the fruit rather than to the leaves of the vine. Starch, dextrine, egg powder, and dried blood failed to increase the adherence of bordeaux mixtures. Resin, soap, potassium silicate, molasses, gum tragacanth, and glue increased the adherence in the order named. In a second paper Perraud (1898) recommends the use of resin dissolved in boiling . sodium carbonate. This material was added when cool to copper sulphate to increase its adherence. Similar results were claimed for a mixture of 2 per cent of copper sulphate and 3 per cent of soap. An actual decrease in the adherence of bordeaux mixture due to the addition of turpentine was noted by Ravaz and Bonnet (1903). Resin slightly increased the adherence, but the difference in both cases was considered unimportant. In many of these investigations, the organic material was added to give both adherence and spreading and many workers believed that a spray which would spread would also adhere better. Vermorel and Dantony (1913) clearly distinguished between these two properties, pointing out that a spray may spread without showing any remarkable adherence, while excellent adherence may occur even if the spray does not spread well. Lafforgue (1913) also distinguishes between spreading and adherence.

These papers represent the development of one method of making fungicides adhere. In many cases the added material reacted with the copper, forming such compounds as copper saccharate, copper stearate, copper resinate, copper caseinate, and copper albuminate. Some of these compounds, colloidal when freshly prepared, gave an increased

adherence as a result of the fineness and insolubility of their particles. The copper, being formed into a stable and insoluble compound, lost much if not all of its fungicidal value. This fact coupled with the physiological effects produced by coating the leaves with an insoluble preparation similar to varnish, resulted in the discontinuance to a very large extent of the use of such materials.

THE USE OF ORGANIC MATERIALS WITH INSECTICIDES

In early experiments with arsenic preparations for the control of insect pests, investigators feared that the material might adhere too long. Spraying for the gypsy moth developed the use of lead arsenate, a slow-acting poison which could be applied in large quantities without injury to the foliage. Because of its low toxicity, it was necessary that it should adhere for a longer period. Fernald (1894) stated that it is highly desirable to add 2 quarts of glucose or molasses to each 150 gallons of water to increase the adherence. The idea of using glucose to cause adherence was possibly the result of the use of sugar with fungicides, but lead arsenate gave no reaction with glucose. Lowe (1896) pointed out that the use of glucose did not increase the adherence of lead arsenate but that glue at the rate of 2 quarts to 45 gallons gave satisfactory results. Kirkland (1898) showed clearly by means of general observation, chemical analysis, and physiological tests on caterpillars, that the addition of glucose did not increase the adherence of lead arsenate. The glucose was washed off the leaves by the first shower.

Washburn (1891) found that the addition of whale oil or soft soap to the spray increased the adherence of paris green, probably because of its more even distribution. A finely divided solid is more adherent, but Marlatt (1897) showed that paris green when very finely pulverized was more injurious to the foliage. Sirrine (1898) recommended the use of a resin-lime mixture to cause paris green and bordeaux mixture to adhere to the leaves of cabbage and cauliflower. This mixture is really a resinate of lime prepared by making a stock solution of resin, fish oil, and lye, to which, after proper dilution, the lime and paris green are added. The paris green adheres to the particles of the calcium resinate and these in turn adhere to the leaves. Volck (1913) used flour paste made of 4 pounds of wheat flour to 100 gallons of water to increase the adherence of sulphur. Larger quantities of flour caused the dry film to scale off, while smaller quantities were insufficient to "stick" the sulphur.

Surface (1905) lists the materials used to increase adherence. These are resin-lime mixture, soap, resin added to kerosene and used in kerosene emulsion, molasses, glue, flour, and salt when used with

lime sulphur. The use of salt is now generally recognized as having no influence on the adherence of lime-sulphur sprays.

Paste lead arsenate was shown by Astruc, Couvergue, and Mahoux (1911) to be more adherent than a freshly prepared suspension of dry lead arsenate. The age of the diluted spray did not appear greatly to influence its adherence.

Parker (1913) pointed out the possibility of using flour paste with lead arsenate to increase the adherence as well as to produce spreading.

A new method of rendering arsenical materials rainproof or more adherent is given in U. S. Patent No. 1166387. The arsenical substance is coated with an insoluble metallic soap, copper stearate in the case of paris green and lead stearate in the case of lead arsenate. These products were marketed for a few years by the International Color Company, generally as a dry powder for dusting purposes, altho they also manufactured a paste form for general spraying.

Lees (1915), interested in lime preparations as cover washes for trees in late winter and early spring, tried to increase the adherence by the addition of various substances. Glue, flour, and farina (potato flour) gave good results. The best results were obtained with a mixture of whiting, starch, glue, and potassium bichromate. In a second paper (1916) he modified the formula, leaving out the starch. The potassium bichromate was added to the mixture because on exposure to light it reacts with glue, rendering it insoluble.

O'Kane, Hadley, and Osgood (1917), in a study of the arsenic retained by fruit after spraying with lead arsenate, give some data as to the actual adherence of lead arsenate. Altho not directly concerned with adherence, the percentage of arsenious oxide was determined on fruit picked from three to five days after spraying and before a rain had occurred. The fruit on other trees was not picked until much later, thus giving data for a comparison of adherence. Fruit picked so carefully that none of the lead arsenate was rubbed off, showed an average of 0.37 milligram of arsenious oxide per apple, from three to five days after spraying and before rain occurred. An average for twenty-five apples, selected as showing the maximum amount of lead arsenate, was 0.77 milligram per apple. Fruit from other trees sprayed at the same time but picked seventy-five days later had 0.08 milligram and those picked after seventy-six days later had 0.11 milligram per apple. These trees were subjected to a total rainfall of 5.01 inches The average amount of arsenious oxide present on the fruit was 25.6 per cent. Fruit sheltered by the leaves would no doubt show a much higher percentage of arsenic than would normally be the case.

Gray (1918) found that the addition of glue to sulphur increased its adherence. The fact that dry lead arsenate was not so adherent as lead arsenate paste and also that the addition of molasses or sugar

reduced the adherence, was confirmed by the experiments of Hartzell (1918). Stearns (1920) showed that the addition of Irish rock moss or calcium caseinate to the spray increased its adherence. Lovett (1920) considers that in general those substances which increase the spreading of a spray will also increase the adherence of the spray material.

THE USE OF INORGANIC SUBSTANCES

The fact that certain inorganic substances adhere to the leaves better than do others was early noted. This fact led to the use of certain inorganic materials to increase the adherence of the spray materials. Compounds of chromium, aluminum, and more particularly iron, have been tried. Kilgore (1911) combined london purple and paris green with ferrous sulphate and ferric chloride, but the mixture was not a success. Arsenious oxide combined with ferrous sulphate or ferric chloride gave a rather soluble mixture which proved injurious to the foliage. In these experiments adherence was not sought but rather a combined insecticide and fungicide. Girard (1892) added aluminum sulphate to bordeaux mixture to produce a greater adherence. The use of aluminum sulphate suggested itself to Girard because of its mordant character, but the results were not sàtisfactory. Fairchild (1894) noted the remarkable adherence of ferrous ferrocyanide. This led to experiments with iron borate, ferric hydrate, and iron sulphide but no such remarkable adherence was noted. Smith (1907) tested an iron arsenate said to be a by-product in the preparation of ore. It contained 45 per cent of arsenious oxide. Used at the rate of 1.25 pounds to 100 gallons it killed the larvae of the elm leaf beetle without injury to the foliage. The plants were sprayed July 17 and on the 18th a heavy rain occurred and another lighter rain on the 20th. Little trace of the material was found on the 22d. Selby (1908) proposed a modified formula for bordeaux mixture in which the amount of copper sulphate was reduced and a large quantity of iron sulphate was added to serve the purposes of a "sticker." The formula was

> Copper sulphate ....2 pounds
> Iron sulphate ....4 pounds
> Quicklime ...:.....................:...............6 pounds
> Water to make 50 gallons.

The spray was rust colored and showed great adherence. He considered that the iron sulphate (probably ferrous) was precipitated by the lime in the form of iron hydroxide. Pickering (1907), how-ever, has shown that the reaction of ferrous sulphate and lime forms a precipitate of a basic iron sulphate, evidently of the formula 10 $FeO.SO_3$. Volck (1909) prepared an iron sulphide spray by adding ferrous sulphate to lime-sulphur solution. The addition of 20 pounds of iron sulphate to 200 gallons of lime-sulphur spray mixture gave a

black muddy precipitate of sulphur, iron sulphide, and calcium sulphate. This spray proved very effective for powdery mildew of apple.

A definite ferrous arsenate was prepared by Vermorel and Dantony (1909). A solution of 400 grams of ferrous sulphate in 10 liters of water was added and stirred into a solution of 400 grams of sodium arsenate in 10 liters of water, until a test paper impregnated with potassium ferro- and ferricyanide became a clear blue color. Diluting this mixture to 100 liters, it contained 200 grams of ferrous arsenate to the hectoliter. On exposure to the air, as in spraying, the ferrous arsenate forms ferroso ferric arsenate and the ferrous hydrate becomes ferric hydroxide. It is pointed out that ferric hydroxide is an antidote for arsenic poisoning, which fact may explain why very large amounts of this preparation were not injurious to the foliage of plants. Vines were not injured by a proportion of 500 grams to a hectoliter; while pears, apples, and prunes were not injured by a spray containing 2 parts in 100. Used at the rate of 100 to 200 grams to 1 hectoliter, ferrous arsenate successfully controlled the codling moth, *Carpocapsa pomonella*, in experiments extending over three years. Vermorel and Dantony (1909), in another paper, point out that ferrous arsenate can not be successfully combined with bordeaux mixture because of the formation of cupric arsenate, which is injurious to the foliage. They also say that ferrous arsenate alone shows great adherence, but that this adherence is reduced if glucose or molasses is added to the spray. Dalmasso (1910) used ferrous arsenate prepared according to the formula of Vermorel and Dantony for grape spraying in Italy, finding it not quite so effective as lead arsenate. No particular adherent properties are recorded. In America, Smith (1910) used a similar ferrous arsenate, successfully controlling the potato beetle and the elm leaf beetle. No special mention is made of the adherence. About this time several insecticide manufacturers put ferrous arsenate on the market in the United States. One of these, analyzed by Bradley (1910), showed 84.25 per cent of water, only 7.37 per cent of arsenic oxide, and 5.51 per cent of ferrous oxide. The dry ferrous arsenate contains from 50 to 55 per cent of arsenic oxide and from 40 to 45 per cent of ferrous oxide. Melander (1911) tested both home-made, and commercial ferrous arsenate for the control of the codling moth. One pound to 125 gallons of water was used, the trees having 0.37 per cent of wormy apples compared with 0.16 per cent for those sprayed with lead arsenate, and 21 per cent for unsprayed trees. Melander said that ferrous arsenate may be successfully combined with lime sulphur. Scott and Siegler (1915) tested ferrous arsenate in both laboratory and field experiments. It was found to be a slow-acting · poison requiring fairly large doses to insure success. On the other hand, it was considered a safe arsenical substance for use on sensitive

plants, even 2 pounds of chemically pure ferrous arsenate to 50 gallons of water being used on beans and peach without injury. High (1915) considered ferrous arsenate a very desirable spray, since it remains in suspension for long periods and shows no injury on delicate foliage. Ferrous arsenite did not show these desirable qualities. Ferrous arsenate was successfully combined with the cactus extract used for spreading.

Howe (1910) tested the iron sulphate–bordeaux mixture recommended by Selby (1908), finding it a less effective fungicide than standard bordeaux mixture, but more adherent and less injurious to the foliage. Waite (1910) used two fungicides containing iron sulphate; One a 3-3-50 bordeaux with 2 pounds of iron sulphate, and the other self-boiled lime sulphur plus 3 pounds of iron sulphate. It was observed that iron sulphide spray adhered so strongly as to give the plants a brownish appearance which did not wear off until picking time. It increased the greenness of the foliage and fruit to such an extent that the fruit was late in ripening. Ballard and Volck (1914) pointed out that the chief value of iron sulphide spray as a fungicide is due to the presence of precipitated sulphur, no claim being made of superior adherence. Stewart (1915) mentions the addition of iron sulphate to lime sulphur to reduce the injury to the plants and to increase the "sticking" quality of the spray. Lees (1915) used aluminum sulphate, iron sulphate, and potassium bichromate with lime to increase its resistance to rain. Aluminum sulphate was introduced because of the gelatinous character of precipitated aluminum hydroxide. In some cases fair results were obtained but they were not equal to those obtained by the use of organic materials such as glue and flour, and hence are not recommended.

In recent years in a few places in the United States a rain-proof arsenical material has been placed on the market. This preparation contains chromium and arsenic, possibly a chromium arsenate, and when mixed with water forms a bluish-green suspensoid. Great adherence is claimed for this product by the manufacturers.

Summarizing the review of the literature it is found that in general a finely divided material will adhere better than a coarse material. The use of organic materials to cause spreading of the spray will increase the adherence, apparently owing in part at least to the more even distribution of the material over the leaf surface. Some investigators have found the use of certain inorganic salts or elements, particularly iron, greatly to increase the adherence of the spray material, while others have failed to obtain these results.

A NEW THEORY OF ADHERENCE

A survey of the literature fails to show any definite theory or any attempt to explain why the adherence of one material to the leaf surface is superior to that of another. It appeared necessary as a point of departure to obtain some idea as to the causes of adherence between different substances. One of the best examples of adherence suggested was that existing between the particles of two oppositely charged colloids. If a colloid exhibiting a negative electric charge is added in the proper proportions to one possessing a positive electric charge, the particles are attracted to each other, forming masses which separate out as a precipitate. An example is the precipitation of a negative arsenious sulphide sol, a colloidal solution, by a positive ferric oxide sol. The colloidal particles of arsenious sulphide adhere strongly to those of ferric oxide. Suspensoids of dye substances also exhibit either positive or negative electric charges, and when two oppositely charged sols are mixed in the proper proportions, a precipitate is formed without any chemical reaction taking place. The question arises as to whether solids when not of colloidal dimensions possess such electric charges. Glass ground to colloidal dimensions exhibits a negative electric charge, and if added to a positive sol in the proper proportions will produce a precipitate. A glass beaker should therefore be negative if it possesses an electric charge. A positive sol placed in a clean glass container will have some of its colloidal particles deposited upon the glass and these adhere so thoroly that they can be removed only by acid. Another example is that of filter paper dipped into a positive sol such as methyl violet. It will be observed that altho the water rises on the filter paper the dye particles do not extend above the surface of the liquid. This is due to their precipitation on contact with the negative filter paper. The paper can be placed in running water and the dye particles will not be washed away. On the other hand, if the paper is placed in a negative indigo sol, the dye rises with the water far above the surface of the liquid and is readily removed by washing in running water.

King (1917), after a general review of all the theories of dyeing, reached the conclusion that the reaction between the fabric having one electric charge and a dye oppositely charged furnished the best explanation of the results obtained in the dye industry. The various negatively charged fabrics are easily dyed by positive dyes; but if a negative dye is to be used, the cloth must be rendered positive by means of a mordant. The mordant is positive and precipitates itself on the negative surface until a new surface with a positive charge is produced. The negative dye will then readily color the cloth. The mordant may be added to the dye in such quantity that the sol becomes positive, when it will give the desired results.

If these electric forces are of sufficient magnitude to cause a dye to adhere to a fabric and withstand numerous washings, then if similar electric charges exist on the leaf and the arsenical materials, they could be utilized to increase the adherence of the spray materials. The first question is, do the leaf and the common arsenical materials in use at present possess electric charges, and, if so, are they the same or opposite in character?
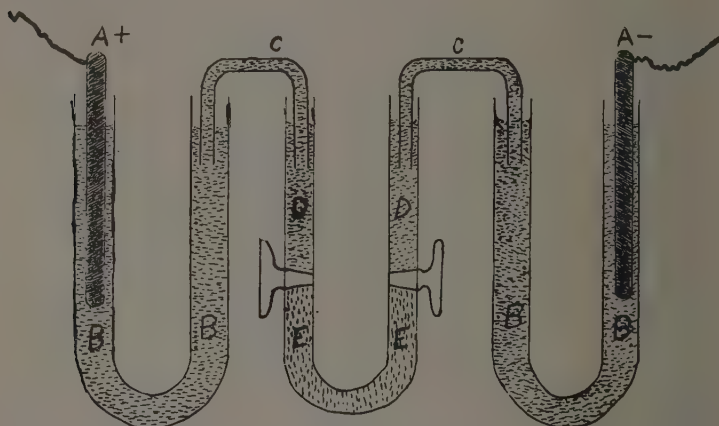
Apparatus Used in Determining the Migration of Particles in the Electric Field
A, electrodes; B, zinc sulphate solution; C and D, tap water; E, suspension to be tested.

ELECTRIC CHARGE EXHIBITED BY COMMON ARSENICAL PREPARATIONS

Methods of testing the charge on the common arsenical preparations found on the market were considered. The first method taken up was the study of the precipitation of sols of known electric charge by suspensions of various arsenites and arsenates. This method, however, may give erroneous results, owing to chemical reactions between the various constituents or to the mutual adsorption of particles with like electric charges. The only method considered free from such objections is the determination of the migration of the particles in the electric field. Sols of the common arsenical materials were prepared by reducing the particles to colloidal dimensions by grinding them with water in an agate mortar. A sol to be tested was placed in a U-tube as shown in the drawing. The stop cocks were closed and the upper end of each arm was washed out and filled with tap water. The tube was then clamped into position and connected with tubes of zinc sulphate, containing the electrodes, by means of small pieces of glass tubing filled with tap water. The level of the liquids was adjusted by connecting

the zinc sulphate containers by means of another piece of tubing containing water. When the level had been established this piece of tubing was removed, the stop cocks were carefully opened, and the current was turned on. It was found possible to use a 220-volt direct current without the introduction of any resistance apparatus. Within half an hour the position of the suspensoid, indicated by its milky or opalescent appearance, was altered by the migration of the particles toward the oppositely charged electrode. Since all these materials carried negative charges, they migrated toward the positive electrode, the level of the suspensoid being raised in the positive arm of the tube and lowered in the negative arm. The rate of migration was faster on one side because of the pull of gravity on the particles, while the rate was retarded on the other side. In each case the position of the electrodes was changed and the direction of migration reversed. Lead arsenate, paris green, zinc arsenite, tri calcium arsenate, and magnesium arsenate were all found to be negative. The addition of calcium hydroxide did not alter the negative charge of calcium arsenate. Which arsenical substance possesses the strongest charge could not be determined by the experiment, since the rate of migration is governed not only by the magnitude of the charge but also by the size of the particles. The rain-proof colloidal preparation containing chromium and arsenic, previously mentioned, was tested, but no definite migration occurred even in two hours' time. This electric neutrality may be due to the presence of dextrin, which acts as a protective colloid.

ELECTRIC CHARGE EXHIBITED BY THE LEAF SURFACE

Having definitely proved by cataphoresis that the common arsenical preparations possess, when wet, an electric charge negative in character, the next question was the demonstration of an electric charge on the leaf surface. Empirically, the leaf should be negative, since filter paper made of cellulose is negative. Cotton, a plant product, is also negative. Stains, which give good results with leaf tissues, either are positive or are prepared with aluminum compounds so that the finished stain is positive. The epidermis of a plant stained with eosin, which is negatively charged, readily washes out in water; while Delafield's Haematoxylin, prepared so that it undoubtedly is positive, is not removed by washing. These statements, however, do not furnish positive proof of the negative character of the leaf. The possibility of determining the charge on the leaf by migration of its particles, after grinding in water, was discarded, because such a test would merely show that the cellulose and proteins of the leaf tissue are negative.

If gelatin in the form of a sol is placed in the electric field, the particles of gelatin migrate toward the electrode opposite in character to the charge carried by the gelatin particles. If a concentrated sol

of gelatin is placed in the bottom of the U-tube and allowed to set to a gel, thus forming a semi-solid barrier, the passage of a current of electricity across the field will no longer be accompanied by a migration of gelatin particles. Under these conditions a flow of water will take place through the gelatin toward the pole with the same sign as the charge carried by the gelatin. The flow of water may be explained by the fact that when a solid takes on a certain electric charge, the water at its surface assumes the opposite sign. This phenomenon, known as electric endosmosis, is well known and is utilized in several industrial processes.

If water could be made to migrate across a leaf surface or through a leaf by endosmosis, it would give positive proof of the presence of an electric charge on the leaf surface. After several unsuccessful attempts the following method gave good results. A bean leaf was bound tightly over one end of a glass tube and the tube partially filled with water. It was then clamped into position with the leaf end immersed in a beaker of water. One electrode was inserted into the tube and the other was placed near the leaf in the beaker. When the current was turned on, the water passed through the leaf, moving in the direction of the negative electrode. Changing the position of the electrodes changes the movement of the water, about half a cubic centimeter passing through the leaf in half an hour. A few minute holes having been pricked in the upper epidermis of a citrus leaf, it was arranged in a similar manner, and the results obtained were even better, since more than a cubic centimeter of water was transferred in half an hour. The better results appeared to be due to the tougher texture of the citrus leaf, which made possible a tighter union with the tube. These experiments show that the leaf surface, when wet, exhibits a negative electric charge.

PREPARATION OF AN ELECTRICALLY POSITIVE ARSENICAL SUBSTANCE

Having shown that the arsenates and arsenites in use at the present time are electrically negative in character and that the leaf surface shows a similar negative charge, the question is presented as to how a positive material may be prepared. Most solids ionize in such a manner that they become negative, and of those which are positive and might be utilized in sprays, only three can be considered.[5] Sols of aluminum, chromium, and iron oxides show the desired positive charge. Of these aluminum and iron appeared the most promising. Two methods of

[5] Besides the three mentioned in this paper, positive arsenicals of lead, zinc, calcium, magnesium, copper, and barium have been made and a patent has been granted on these products.

ᵢᵢ their utilization were suggested: (1) spraying the leaves wi h the posi-
tive material, followed by the application of the negative arsenical ma-
terial; and (2) the addition of sufficient positive material to the arsen-
ical suspension to make the whole mixture positive in character. The
first method is impractical, as it would require two sprayings of the
plant. Aluminum hydroxide was precipitated by adding ammonium
hydroxide to aluminum chloride, care being taken that not all of the
chloride was converted into the hydroxide. A precipitate of aluminum
hydroxide is readily peptized by aluminum chloride forming a positive
sol. By filtering the precipitate, but not washing it, enough chloride
remained to make the material electrically positive. In a preliminary
test, a quantity of this aluminum hydroxide was mixed with lead
arsenate and sprayed on young citrus trees in the greenhouse. To
serve as a check, similar trees were sprayed with lead arsenate alone.
After drying, some of the plants from each set were washed by a strong
stream of water from a hose for five hours. A macroscopic examina-
tion showed practically none of the spray material on the leaves sprayed
with the lead arsenate alone, while the leaves of those sprayed with the
lead arsenate–aluminum hydroxide mixture were similar in appearance
to the check plants which had not been washed. Similar results were
obtained by addition of ferric hydroxide to lead arsenate. The substi-
tution of geranium plants for citrus trees gave comparable results.

It would be difficult to make an estimate of the exact quantity neces-
sary to give the desired results. The reactions taking place are more
easily demonstrated by two colloids possessing opposite electric charges.
An illustration would be the reaction of a negative sol of arsenious
sulphide with a positive sol of ferric oxide. One particle of the ferric
oxide carrying three positive charges would tend to neutralize the
charges of three arsenious sulphide particles, since these carry only
one negative charge. When a quantity of the ferric sol is added to an
arsenious sulphide sol in such proportions that all the negative charges
are not neutralized, no precipitation occurs and the mixture is negative.
If the number of positive and negative charges is equal or nearly equal,
the mixture produces electric neutrality and a precipitate is formed.
If enough ferric oxide is added to produce an excess of positive charges,
the mixture remains clear and is positive in character. This latter con-
dition is the one sought when aluminum hydroxide or ferric hydroxide
is added to lead arsenate to increase its adherence.

Owing to these difficulties, an effort was made to prepare an arsenical
substance which would itself be positive. Grimaux (1884) showed
that the precipitate formed when ferric chloride is added to sodium ar-
senate or sodium arsenite may be peptized, forming a sol which on
dialysis gave a basic ferric arsenate, $Fe_2 (AsO_4)$. Recently, Holmes

and Rindfusz (1911), Holmes and Arnold (1918), and Holmes and Fall (1919) have studied the preparation of ferric arsenate sols and gels. It is possible to prepare similar preparations of aluminum and chromium. In none of these papers is there any mention of the character of the electric charge carried by the particles of the ferric, aluminum, or chromium arsenate. Sols of ferric arsenate and arsenite, aluminum arsenate and arsenite, and chromium arsenate prepared in a similar manner were found to be electrically positive. Ferric arsenate precipitated by adding 90 parts of a one-fifth molar solution of sodium arsenate to 100 parts of a one-fifth molar solution of ferric chloride was centrifuged, washed, and the paste dried. This material, ground to colloidal dimensions, showed a migration of the particles toward the negative poles, demonstrating that they carry a positive electric charge. Aluminum arsenate similarly prepared showed a slight migration toward the negative pole. These and several other arsenical materials were used in a field test of adherence.

FIELD TESTS OF ADHERENCE

The test of the adherence of different preparations was made on potato plants. The potatoes were in an open field exposed to wind, dew, and rain. During heavy showers, soil was splashed over the plants and washed off again, actually tending to scour the leaves. In the cultivation of the plants, soil was frequently thrown over the leaves, thus tending to remove the spray materials.

The following preparations were used in the proportions given, the amount of each material being figured on a dry basis.

TABLE I

	Pounds	to Gallons
Lead arsenate powder..	1.5	50
Calcium arsenate powder...	1.5	50
Zinc arsenite powder..	1.5	50
Magnesium arsenate powder...	1.5	50
Paris green powder..	1.5	50
Lead arsenate powder, 1.5 lbs. + ferric hydroxide paste, 0.4 lb. (dry weight)		50
Ferric arsenate paste...	2.0	50
Ferric arsenite paste...	2.0	50
Ferrous arsenate paste..	2.0	50
Aluminum arsenate paste...	1.0	50

The materials were applied to one or two rows of potatoes and several rows throughout the plot were left unsprayed to serve as checks. When the sprayed plants were dry, ten representative leaves were collected from each set to be analyzed for arsenic. There was no rain for six days after the sprays were applied and then only 0.06 inch fell, hence all the compounds had an excellent opportunity to destroy the potato beetle larvae. Nine days after spraying the check plants were completely stripped of leaves and a count of larvae on the sprayed plants gave the results shown in Table II.

TABLE II

	Average per plant
Lead arsenate..	2.5
Calcium arsenite...	0.7
Zinc arsenite..	0.4
Magnesium arsenate..	0.3
Paris green..	1.0
Lead arsenate + ferric hydroxide..	9.6
Ferric arsenate..	2.4
Ferric arsenite..	0.2
Ferrous arsenate...	1.6
Aluminum arsenate..	2.1

Some of these averages are high, owing to the proximity of check rows where the larvae, having stripped the plants, were migrating to adjacent rows. A count on part of the lead arsenate row next to a check row showed an average of four larvae per plant, while that part not adjoining the check row had an average of one larva per plant. This condition existed in the rows sprayed with ferric arsenate, ferrous arsenate, and aluminum arsenate, but not in the row treated with lead arsenate–ferric hydroxide mixture.

In the preparation of the lead arsenate–ferric hydroxide mixture there was a decided tendency for the particles to form masses which were extremely difficult to hold in suspension. The first six plants in the row obtained a very heavy dose of the spray materials while the rest of the row received very little. For this reason in the analysis of the plants, the first six plants in this set were kept separate from the others. In the analysis of the plant material for arsenic, the organic material was oxidized by boiling with nitric and sulphuric acids. The arsenic was determined by the Gutzeit method (Scott, 1917). The leaves of the plants, taken immediately after the spray had dried, represented 100 per cent of the spray material. Other determinations were made on leaves collected seven, eleven, and seventeen days after spraying, the average amount per leaf in terms of arsenious oxide being recorded in Table III. In this table is also given a record of the rainfall during this period.

Reviewing the field test, a relationship between the adherence and the electric charge is quite apparent. Lead arsenate, which adhered best of those possessing a negative electric charge, showed only 6.6 per cent at the close of the experiment. Aluminum arsenate tested in the electric field was only very slightly positive, since only a slight migration of the particles occurred. Ferrous arsenate was negative, but on the plant decomposition would produce ferric arsenate and ferric hydroxide according to Vermorel and Dantony (1909). The decomposed material would then no doubt be positive. No definite data are available concerning the charge possessed by particles of the lead arsenate–ferric hydroxide mixture, but it was mixed in proportions

which should form a positive material. Ferric arsenate was considered the most promising of the entire set, but its use requires further investigation.

TABLE III

	After spray-ing	6 days	7 days	Per cent of total	10 days	11 days	Per cent of total	16 days	17 days	Per cent of total	Total rain-fall
	Mg.	·	Mg.	·	·	Mg.			Mg.	¹	
Lead arsenate........	0.75	...	0.10	40.0	...	0.200	26.6	...	0.050	6.6	...
Calcium arsenate.....	1.00	...	0.10	10.0	...	0.050	5.0	...	0.050	5.0	...
Zinc arsenite.........	1.40	...	0.35	25.0	...	0.125	8.9	...	0.075	5.35	...
Magnesium arsenate...	1.25	...	0.15	12.0	...	0.075	6.0	...	0.025	2.0	...
Paris green...........	1.60	...	0.10	6.2	...	0.075	4.6	...	0.025	1.5	...
Lead arsenate + fer-ric hydroxide											
First 6 plants....	8.00	...	2.40	30.0	...	...	...	...	1.400	17.5	...
Other plants......	0.65	...	0.20	30.7	...	0.100	15.3	...	0.100	15.3	...
Ferric arsenate.......	1.20	...	0.60	50.0	...	0.400	33.3	...	0.200	16.6	...
Ferric arsenite........	2.40	...	0.75	31.2	...	0.600	25.0	...	0.300	12.5	...
Ferrous arsenate......	2.80	...	1.25	44.6	...	0.750	26.7	...	0.350	12.5	...
Aluminum arsenate...	0.75	...	0.15	20.0	...	0.075	10.0	...	0.075	10.0	...
	In.		In.		In.			In.			In.
Rainfall	...	0.06	0.03	...	0.80	...	...	2.18*	...	...	3.07

* This record represents one severe storm.

The poor adherence of calcium arsenate is of particular interest. Graham (1918) found it to adhere better than lead arsenate, while Wilson (1919) also considered it equal in adherence to lead arsenate. Graham's tests were conducted in the greenhouse and hard water was used to wash off the arsenical materials. Owing to the presence of the common calcium ion, the presence of calcium carbonate in the tap water would reduce the solubility and the rate of decomposition of the calcium arsenate. Wilson applied the calcium arsenate with lime and a similar effect was obtained. In these experiments, the calcium arsenate was used alone, and apparently rapidly dissolved, decomposed, and disappeared from the leaves.

PREPARATION OF POSITIVELY CHARGED FERRIC ARSENATE

In further investigations with ferric arsenate it was found that it did not always possess a positive electric charge, in fact it was often neutral or even negative. An effort was made to discover under what conditions the best material could be prepared. Grimaux (1894) considered the first precipitate formed by the addition of sodium arsenate to ferric chloride as represented by the formula $(AsO_4H)_3Fe_2$. When this material was peptized by ferric chloride, a reaction was obtained represented by the following equation:

$$2(AsO_4H)_3Fe_2 + Fe_2Cl_6 = 3 \ (AsO_4H)_2 \ Fe_2Cl_2$$
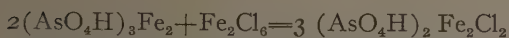
Upon dialyzing this sol a basic compound of ferric arsenate was retained by the membrane while hydrochloric acid passed through. Holmes and Arnold (1918) noted that the appearance of the gel obtained on dialysis depended upon the proportion of ferric chloride used in the peptization of the ferric arsenate precipitate. If a large quantity was used the gel obtained was reddish or reddish-brown, while if only a small quantity was used the gel was a dirty yellowish color. A study of these materials and the character of the charge carried by their particles should throw light upon the problem.

Three different sols were prepared, the first, which will be referred to as the 50-45, was made by adding slowly to 50 cubic centimeters of a one-fifth molar solution of ferric chloride, 45 cubic centimeters of a one-fifth molar solution of disodium arsenate, the precipitate being peptized as rapidly as it formed. The second was similarly prepared, but only 35 cubic centimeters of the arsenate was added, while 25 cubic centimeters was added to the third. These were known as the 50-35 and the 50-25 sols. The 50-45 sol was light yellow with greenish tints and somewhat clouded. The 50-35 and 50-25 sols were perfectly clear and of a deep yellow color with greenish tints. The three different sols were dialized in separate containers by means of collodion sacs. Only distilled water was used and all the wash water was saved for analysis. Having determined the amount of Cl, AsO_4, and Fe present in the original sols, a fairly accurate knowledge of the composition of the gel was obtained by the analysis of the wash water.

Hydrogen sulphide was first passed through the solution to remove the arsenic. This required considerable time to insure its complete removal. The arsenious sulphide was filtered off, redissolved, and the quantity of arsenic finally determined by iodine titration. The filtrate was made up to 1,000 cubic centimeters and a portion used for the determination of the ferrous iron by titration with potassium permanganate. The chlorine was titrated with silver nitrate, using potassium chromate as an indicator. Considerable difficulty was experienced with this method since the indicator did not indicate the end point, more chlorine being found than had existed in the original sol. A double titration method using an excess of silver nitrate and then determining this excess by titration with ammonium thiocyanate using ferric sulphate as an indicator gave better results. The three different sols may be represented by the following equations based upon the results of the analyses.

50-25 Sol
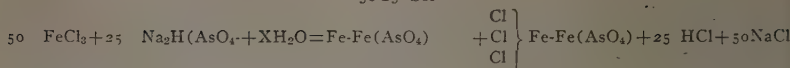
$$50 \ FeCl_3 + 25 \ Na_2H(AsO_4 + XH_2O = Fe\text{-}Fe(AsO_4) \qquad \left. \begin{array}{c} Cl \\ +Cl \\ Cl \end{array} \right\} Fe\text{-}Fe(AsO_4) + 25 \ HCl + 50 NaCl$$

$Fe. = 0.60256$ g.	$Fe = 0.1344$ g.	
$Cl. = 1.0476$ g.	$AsO_4 = 0.1530$ g.	$Fe = 0.46816$ g.
$AsO_4 = 0.7006$ g.	(Colloid)	$AsO_4 = 0.5476$ g.
		$Cl = 1.0415$ g.

(Passed through membrane
crystalloid)

50-35 Sol
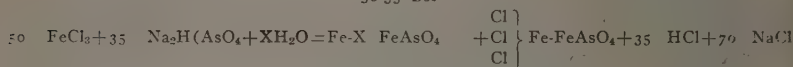
$$50 \ FeCl_3 + 35 \ Na_2H(AsO_4 + XH_2O = Fe\text{-}X \ FeAsO_4 \qquad \left. \begin{array}{c} Cl \\ +Cl \\ Cl \end{array} \right\} Fe\text{-}FeAsO_4 + 35 \ HCl + 70 \ NaCl$$

$Fe = 0.60256$ g.	$Fe = 0.22624$ g.	$Fe = 0.37632$ g.
$Cl = 1.0476$ g.	$AsO_4 = 0.50064$ g.	$AsO_4 = 0.4802$ g.
$AsO_4 = 0.98084$ g.	(Colloid)	$Cl = 1.0437$ g.

(Crystalloid)

50-45 Sol
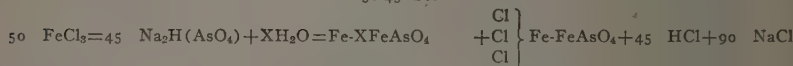
$$50 \ FeCl_3 = 45 \ Na_2H(AsO_4) + XH_2O = Fe\text{-}XFeAsO_4 \qquad \left. \begin{array}{c} Cl \\ +Cl \\ Cl \end{array} \right\} Fe\text{-}FeAsO_4 + 45 \ HCl + 90 \ NaCl$$

$Fe = 0.60256$ g.	$Fe = 0.56566$ g.	$Fe = 0.0369$ g.
$Cl = 1.0476$ g.	$AsO_4 = 1.20703$ g.	$AsO_4 = 0.05405$ g.
$AsO_4 = 1.26108$ g.	(Colloid)	$Cl = 1.03143$ g.

(Crystalloid)

From these equations it appears that there is a compound of ferric arsenate and ferric chloride formed which is capable of passing through a dializing membrane.[6] The proportions in all three cases show that this compound is made up of one molecule of ferric chloride and one of ferric arsenate, $Cl_3Fe\text{-}Fe \ (AsO_4)$. The proportions of ferric arsenate of iron in the colloid, however, vary. In the 50-25 it apparently may be represented by the formula $Fe\text{-}FeAsO_4$, while in the other gels a larger quantity of ferric arsenate is present and the formula may be represented by Fe X Fe $(AsO_4)_2$. The 50-25 formula appears to be ferric oxide with an adsorbed molecule of ferric arsenate. The 50-35 and 50-45 may contain ferric oxide with an X number of adsorbed ferric arsenate molecules or it may consist of $Fe\text{-}FeAsO_4$ with a number of unadsorbed ferric arsenate molecules. The 50-45 sol set to a gel when dialyzed from ten to fifteen hours, and was a rather opaque dirty yellow mass. The 50-35 and 50-25, after two to three days dialysis, finally formed a clear reddish gel.

The three gels were carefully dried, and after grinding to colloidal dimensions their migration in the electric field was determined. Both the 50-45 and the 50-35 migrated toward the positive pole and therefore possessed a negative charge. The 50-25 sol, being positive, migrated toward the negative pole. All three sols before dializing had particles carrying positive charges.

[6] Arsenic acid may be liberated by the stronger hydroclric acid, and the material which passes through the membrane may consist of a mixture of ferric cloride and arsenic acid. If such is the case, it is not apparent why this arsenic acid should be reduced in quantity by the addition of sodium arsenate.

From these results it would appear that the pure or nearly pure ferric arsenate was negative, while if ferric chloride or ferric oxide is present with it, the particles possess a positive charge. Ferric arsenate prepared from equal molecular portions of disodium arsenate and ferric chloride was filtered, washed, dried, and prepared as a suspensoid by grinding. This material was negative. The addition of ferric chloride equal in weight to the ferric arsenate present in the suspensoid, caused it to take on a strong positive charge. Holmes and Fall (1919) have shown that the amount of ferric chloride necessary to peptize a given quantity of ferric arsenate increases rapidly with the age of the precipitate up to one or two days, with only a smaller further increase being noted with older precipitates. This was found to be due to a decrease in the hydration of the precipitate and in the formation of larger aggregates with a consequent decrease in the external surface of the particles. In the present investigation it was found to be impossible to peptize with ferric chloride a precipitate which had been thoroly dried. However, as already shown, the ferric chloride is able to give the particles a positive charge, due apparently to a reaction with the surface of the particles. The amount necessary to give the desired results will vary with the surface area of the particles. The quantity necessary to produce a positive charge on the surface of large particles such as are present in the spray suspension, will be much less than is required where the surfaces are greatly increased by reducing the size of the particles to colloidal dimensions. The minimum quantity that may be used to give the desired adherence to a ferric arsenate spray, remains to be determined by further tests in later investigations.

Holmes and Rindfusz (1916) showed that ferric arsenate may be peptized by ammonium and other hydroxides, apparently a ferric oxide with an adsorbed arsenate being produced. This method has been tried and gives a positive material but is undesirable, since the presence of large quantities of ferric oxide reduces the toxicity of the mixture.

COMPARATIVE TOXICITY OF DIFFERENT ARSENICAL PREPARATIONS

Freshly precipitated ferric hydroxide is a well-known antidote for arsenical poisoning in higher animals (Sollmann, 1917). The reaction between ferric hydroxide and arsenious oxide was first thought to be due to the formation of a basic ferric arsenate, but Biltz (1904) has shown that the ferric hydroxide adsorbs the arsenious oxide and does not form a definite compound. Vermorel and Dantony (1909) stated that ferrous arsenate on the plant was decomposed with the formation of ferric hydroxide. Scott and Siegler (1915) found ferrous arsenate low in toxicity. In view of these facts it was considered advisable to

obtain some idea of the toxicity of these new preparations in comparison with other common arsenical compounds.

METHODS OF DETERMINING COMPARATIVE TOXICITY

A short review of the literature dealing with toxicity presents several methods of obtaining a comparison of toxicity. Marlatt (1897) studied the toxicity of paris green, london purple, and copper arsenate, using as a basis of comparison the time required to kill the insects and the total number killed. Holloway (1912) attempted to express the toxicity numerically. Paris green at the rate of two milligrams per leaf was taken as a standard. The toxic value was expressed in the period of time required to kill. If a given poison required twice as long as paris green to produce death, then its toxic value would be expressed as 0.5, while a poison killing more quickly than the standard would be represented by a number greater than 1. This value was called the poison exponent. Mention is made of iron arsenate having a poison exponent for *Heliothus obsoleta* of 0.5 for the first instar, 0.33+ for the second, 0.81 for the third, and 0.47+ for the fourth, fifth, and sixth instars. Scott and Siegler (1915) compared the killing values of various arsenical compounds by measuring in square inches the amount of leaf surface consumed by the fall webworm, *Hyphantria cunea* (Drury), feeding on black cherry, *Prunus serotina*. The time required to produce death was also taken into consideration. They consider lead arsenate as the best arsenical compound, but the triplumbic form is a slow acting poison. No attempt is made to arrange the preparations in the order of their toxicity and such an arrangement would be difficult, owing to the variation in quantity of the poisons used. Tartar and Wilson (1915) studied the comparative toxicity of lead hydrogen arsenate and basic lead arsenate. An arsenic analysis was made of the tissues of the dead insects, showing that those killed by the acid lead arsenate contained more arsenic. This was considered due to the more rapid adsorption of the chemically reactive diplumbic form, while the triplumbic lead arsenate was passed through the intestinal tract without much absorption taking place. Sanders and Brittain (1916) based their comparison of toxicity upon the percentage of larvae dead after feeding on sprayed foliage for a certain arbitrary number of days. Lovett and Robinson (1907), continuing the investigations started by Lovett and Wilson (1915), take into consideration the time required to kill, the approximate amount of the arsenical compound necessary to produce death, and the ratio of arsenic pentoxide in the tissues to that in the excrement. The ratio of lead hydrogen arsenate is given as 1 to 0.544, calcium arsenate 1 to 0.70, and basic lead arsenate 1 to 1.51.

COMPARATIVE TESTS OF TOXICITY

In the present work, locusts, *Melanoplus femur-rubrum*, were fed upon a standard mixture composed of 1 gram of bran to 0.5 gram of sugar, 1.5 cubic centimeters of water, and 0.04 gram of the poison to be tested. When the mixture became dry it was moistened with a few drops of water. Large glass cylinders covered with cheese-cloth at the top were used as feeding cages. Each cage contained ten insects. Numerous observations were made, and the number of dead locusts was recorded. When all were dead in any experiment their bodies and their excreta were separately collected, dried, and preserved for analysis. The experiments with each poison were repeated five times, hence the figures given represent the average for fifty locusts. The relative merit of the different methods of comparing toxicity may be judged from the data presented, which are based upon the time required to kill, the amount of bran mash consumed, and the ratio of the poison found in the body and in the excreta. The organic matter was destroyed by boiling with nitric and sulphuric acid and the arsenic determined by the Gutzeit method. (Scott 1917). The data have been compiled in the following tables, where the materials are arranged in order of their toxicity, the most toxic substance being placed first.

These tables show clearly that the best basis of comparison is the ratio of the quantity of the chemical found in the body to that found in the excreta. This point is confirmed by feeding mixtures containing different quantities of the same chemical.

TABLE IV

TOXICITY BASED ON NUMBER OF GRAMS OF BRAN MASH CONSUMED BEFORE DEATH*

Calcium arsenate	0.0045060
Sodium arsenite	0.0051975
Calcium arsenite	0.0052730
Paris green	0.0056700
Ferric arsenite	0.0058905
Colloidal aluminum arsenate	0.0060705
Zinc arsenite	0.0061905
Colloidal ferric arsenate	0.0063370
Magnesium arsenate	0.0077400
Stearated paris green	0.0077400
Ferric arsenate	0.0078000
Sodium arsenate	0.0078000
Aluminum arsenate	0.0083610
Arsenious oxide	0.0116700
Ferrous arsenate	0.0120000
Lead arsenate	0.0210000

* Calculated from the sum of the arsenic recovered from the bodies and excreta and the proportion of arsenic present in the mash.

TABLE V

TOXICITY BASED ON THE AVERAGE NUMBER OF HOURS NECESSARY TO PRODUCE DEATH

Sodium arsenite	20.1
Calcium arsenite	25.5
Stearated paris green	30.3
Arsenious oxide	33.0
Sodium arsenate	37.5
Paris green	38.1
Magnesium arsenate	44.7
Calcium arsenate	45.2
Ferric arsenate	46.7
Zinc arsenite	46.7
Colloidal aluminum arsenate	57.2
Colloidal ferric arsenate	57.9
Ferric arsenite	60.6
Aluminum arsenate	67.2
Ferrous arsenate	70.0
Lead arsenate	92.2

TABLE VI

TOXICITY BASED ON THE RATIO OF THE CHEMICAL IN THE BODY AND IN THE EXCRETA

Chemical	Milligrams in excreta	Milligrams in body	Excreta Ratio ——— Body
Arsenious oxide	0.005600	0.15000	0.037334
Sodium arsenite	0.004330	0.11110	0.039000
Colloidal aluminum arsenate	0.006051	0.15130	0.039995
Sodium arsenate	0.010000	0.25000	0.040000
Magnesium arsenate	0.006400	0.16000	0.040000
Calcium arsenate	0.005290	0.13200	0.040077
Colloidal ferric arsenate	0.011440	0.21440	0.053360
Calcium arsenite	0.006100	0.11000	0.055455
Stearated paris green	0.010900	0.16000	0.068130
Ferric arsenite	0.010578	0.13210	0.080077
Zinc arsenite	0.017800	0.13210	0.134750
Paris green	0.015000	0.11000	0.136370
Ferric arsenate	0.048000	0.16000	0.300000
Aluminum arsenate	0.047160	0.13830	0.341240
Ferrous arsenate	0.120000	0.20000	0.600000
Lead arsenate	0.486660	0.44333	1.097700

TABLE VII

Grams of lead arsenate added to bran mash	Grams of bran consumed before death	Hours required kill	Excreta Ratio ——— Body
0.02	0.0300	66.5	1.0000
0.04	0.0210	92.2	1.0998
0.10	0.0108	69.5	1.2005
0.20	0.0090	55.5	1.2502
0.30	0.0070	58.0	0.9092

The hours required to produce death vary greatly while the quantity consumed is reduced rapidly. On the other hand, the results are affected but slightly by great differences in the quantity of the poison fed to the locusts.

A METHOD OF EXPRESSING TOXICITY

*Incidentally this method opens up a possibility of directly comparing arsenical compounds, giving them a definite numerical value in comparison with some standard compound of arsenic. In the present investigation, the object was merely to obtain an idea of the relative toxicity of certain new arsenical materials compared with those in use at the present time. By taking the reciprocal of the number obtained by dividing the quantity of the chemical in the excreta by that found in the body, the most toxic chemical becomes the one with the highest numerical value, as is shown in Table VIII.

TABLE VIII

	Reciprocal of the ratio	Value when lead arsenate $= 1$
Arsenious oxide..	26.78500	29.4010
Sodium arsenite.......................................	25.64100	28.1460
Colloidal aluminum arsenate..........................	25.00000	27.4430
Sodium arsenate.......................................	25.00000	27.4430
Magnesium arsenate...................................	25.00000	27.4430
Calcium arsenate......................................	24.95200	27.3890
Colloidal ferric arsenate.............................	18.74000	20.5710
Calcium arsenite......................................	18.03200	19.7940
Stearated paris green.................................	14.78000	16.1120
Ferric arsenite.......................................	12.48800	13.7070
Zinc arsenite...	7.42110	8.1462
Paris green...	7.33330	8.0494
Ferric arsenate.......................................	3.33330	3.6590
Aluminum arsenate....................................	2.93050	3.2169
Ferrous arsenate......................................	1.66660	1.8295
Lead arsenate...	0.91099	1.0000

Assuming the value of the lead arsenate to be 1 instead of 0.91099 it is simple to express the toxicity of any of the other arsenical compounds in terms of lead arsenate. Ferric arsenate would then have a value of 3.659, or in other words, would be more than three times as toxic as lead arsenate, while paris green would be eight times, and arsenious oxide more than twenty-nine times as toxic as lead arsenate. Selecting absolutely pure lead arsenate as a standard, several common insects could be fed under definite conditions and a numerical value applied to any compound of arsenic placed on the market.

The values presented in this paper can not be used in this manner, as the lead arsenate used was a commercial product and not chemically pure.

INFLUENCE OF FERRIC HYDROXIDE ON TOXICITY

The results obtained by the addition of ferric hydroxide to arsenious oxide are recorded in Table IX.

TABLE IX

	Ratio Chem. in excreta
	Chem. in body
Arsenious oxide 0.04 gram..	0.037334
Arsenious oxide 0.04 g. + stale ferric hydroxide paste containing 0.1614 g. dry weight..	0.056000
Arsenious oxide 0.04 g. + colloidal ferric oxide containing 0.0647 g. of dry material..	0.133333
Arsenious oxide 0.04 g. + fresh ferric hydroxide paste containing 0.1714 g. dry weight..	0.333333
Arsenious oxide 0.04 g. ± fresh ferric hydroxide paste containing 0.1714 g. dry weight, but allowed to stand mixed for 48 hours before feeding....	0.600060

The data show clearly that the addition of ferric hydroxide which adsorbs arsenious oxide reduces the toxicity of the mixture. Calcium hydroxide mixed in the same way gave a ratio of 0.05 compared with calcium arsenite with a ratio of 0.055455. In this case the two reacted, giving calcium arsenite with a ratio checking with the ratio of calcium arsenite previously tested. None of the figures given in the table check with ferric arsenite having a ratio of 0.080077. This compound is apparently not formed.

The addition of ferric hydroxide to other arsenical compounds gave similar results. Sodium arsenate with a ratio of 0.039 was reduced by the addition of ferric hydroxide to 0.1333, while paris green 0.13637 became 0.74834.

These experiments explain the cause of the low toxicity of ferrous arsenate. Ferric arsenate is not so low in toxicity, but the addition of ferric hydroxide in any large quantity to increase the positive electric charge would no doubt reduce its toxicity. The adsorption of arsenic preparations by ferric hydroxide may be the explanation of the lack of injury to bean and peach foliage recorded by Scott and Siegler (1915). It has not been possible to investigate this phase of the subject at the present time.

CONCLUSION REGARDING THE PHENOMENON OF ADHERENCE

In that portion of the present investigation dealing with the adherence of spray materials to the leaf, it has been demonstrated that the leaf surface assumes, when wet, a negative electric charge and that suspensoids of the common arsenic compounds ionize in such a way that their particles are also negative. Based upon the results obtained in the dye industry, the assumption is made that spray materials carrying positive electric charges would adhere to the negatively charged leaf surface better than materials exhibiting negative charges. Field tests have confirmed this assumption. Positive arsenic preparations

of different elements were prepared and tested, ferric arsenate being considered the most promising material. The presence of ferric hydroxide in the spray material is not desirable since, owing to its adsorption of arsenic, it lowers the toxicity of the preparation.

Many phases of the problem remain to be solved by future investigations. One of the most important questions is the successful combination of a positive ferric arsenate with a spreader to give the mixture both spreading and adherent properties. Organic materials which produce a film of the spray on the surface of waxy leaves should have no influence on the electric charge, but the protein type of spreader may have a decided effect. Since most emulsoids, such as gelatin, casein, and proteins, act as protective colloids, their addition to the spray might result in the complete loss of the electric charge. On the other hand, a mutual precipitation may occur (Bancroft, 1920), or if the positive charges are in excess the material may retain its positive character. Only field tests will solve these problems.

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The University of Minnesota
Agricultural Experiment Station

Respiration of Shelled Corn

By C. H. Bailey
Division of Agricultural Biochemistry

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INTRODUCTION

Shelled indian corn, or maize, the caryopsis or grain of *Zea mays,* presents an unusual hazard in marketing. Considerable quantities of this cereal are damaged each season as the result of heating when shipped or stored in bulk. About fifteen years ago the European buyers of corn reported that millions of bushels of American corn were discharged at continental ports in a damaged condition, and as a result of their representations the United States Department of Agriculture began a study of the problem. Duvel (1909)[1] reports observations made on bulk corn stored in a Baltimore elevator, the temperature of which reached 133° F. about 8 inches below the surface when left undisturbed from February 17 and 18 to April 27, 1909. From the bottom to a point about two-thirds of the distance to the top of the bin, corn of practically the same character as the surface layer did not change temperature appreciably, but remained cool and sound. Heating corn near the surface of the grain in the bin was so badly damaged that many of the germs were badly discolored, and the average germination was only 10.3 per cent. Corn from the lower 45 feet of the bin gave an average germination of 80.8 per cent at the beginning of the experiment, 71.4 per cent when drawn from the bin, and 81.4 per cent after being handled and dried.

Shanahan, Boerner, and Leighty (1910) state that on examining thirty-four cargoes of corn on arrival at eight of the principal European ports, an average of 12.1 per cent of the corn on board was in a heating or hot condition. Part of this damage could probably, in certain instances, have been obviated by better methods of storage, or by more rapid transit.

Duvel and Duval (1911) stored corn in the hopper scale of a Baltimore elevator on January 5, 1910, and on May 2 the surface layer reached a temperature of 138° F. The same authors (1913) report several series of experiments with corn while in cars in transit. In the first series, beginning April 14, 1910, one car of corn with an initial temperature of 58° F. reached a temperature of 142° F. on May 2, 1910. Corn with a higher moisture content did not change temperature in box cars between December 24, 1910, and January 20,

[1] Bibliographic citations in parentheses refer to "Literature Cited," page 40.

1911, while in a third series of experiments between March 2 and March 29, 1911, one car changed temperature from 40.8° F. at the time of loading to 112° when unloaded. A fourth series loaded in cars May 11 and unloaded June 1, 1911, was affected much like the first, the temperature of the damp corn being 64.2° F. when loaded, and 129° when unloaded.

Boerner (1919) presents the detailed observations of numerous transoceanic corn shipments. Temperatures as high as 146-147° F. were observed in portions of certain cargoes at the time of arrival in Europe, and considerable percentages of many cargoes were badly damaged in consequence of heating in transit.

The investigations cited establish the fact that corn may heat and undergo serious damage when stored in elevator bins, or while in transit in cars or in holds of vessels. Increases in the volume of shelled corn handled in commerce have contributed to the difficulties of its safe transportation and storage. Combined with this has been an apparent tendency on the part of producers to grow large-eared, late-maturing varieties of corn which contain comparatively high percentages of moisture at the time they are shelled for fall marketing. The Office of Grain Standardization (1913) of the United States Department of Agriculture published diagrams indicating that the average moisture content of corn received at Baltimore, Chicago, and New Orleans ranged between about 18.5 and 20.5 per cent during November, December, January, February, and March of the four crop years from November, 1909, to March, 1913. The shelled corn marketed later in these several seasons contained appreciably less moisture, the average being about 13 per cent or less by August. The reason for the regular seasonal variation in the moisture content of commercial corn is found in the more or less continuous drying which the corn undergoes during the months following harvest, since even during the winter ear corn dries gradually if stored in well-ventilated cribs.

RELATION OF RESPIRATION TO HEATING OF GRAIN

It is generally agreed by physiologists that energy for many physiological processes and reactions is released in living cells in an exothermic reaction or succession of reactions known collectively as respiration. In normal or aerobic respiration, oxygen of the atmosphere diffuses or is otherwise conducted to the cells where respiration occurs, and is there involved in a process of oxidation of which water and carbon dioxid are the characteristic end-products. The carbon dioxid which is formed diffuses, or is conducted from such cells to the atmosphere surrounding the organism. The quantity of carbon dioxid respired bears a fairly definite relation to the quantity of heat energy liberated,

and can be converted into terms of calories of heat through the use of a simple factor. Anaerobic respiration, which occurs in the absence of atmospheric oxygen, presumably utilizes the oxygen of certain compounds which are present, in the production of completely oxidized end-products such as carbon dioxid, while at the same time partially oxidized and reduced compounds are produced which are of different character in the different species thus respiring. Enzyms are assumed to be in a measure responsible for the reactions involved in respiration, altho no one has succeeded in simulating such reactions outside the living cell through the use of enzym preparations. Certain physiologists include respiration as one of the criteria of "life," but there is also evidence that respiration occurs in certain organisms which are "dead" as judged by ordinary standards. This fact is of significance in connection with the respiration of damaged corn kernels which are no longer viable.

Investigations of Langworthy and Milner (1913), and Gore (1914) with bananas, and of Hasselbring and Hawkins (1915) with sweet potatoes support the views of Borodin (1876), Maige and Nicolas (1910), and others that in normal plant tissues containing simple hexose sugars, such sugars are the principal substances oxidized. Palladin (1918) says "Regarding the cell as a factory, carbohydrates are the coal and the protoplasm is the machinery" (p. 208).

Germ or embryo cells are evidently the location of most of the respiration occuring in a typical grain. Burlakov (1897) found that 100 grams of soaked wheat grains respired at the rate of 15.2 milligrams of carbon dioxid per hour, while the same weight of embryos respired at the rate of 241.8 mgm. of carbon dioxid per hour. Karchevski (1901) reports a ratio of about 1 to 12 in the comparative rate of respiration of wheat kernels and the germs or embryos. Palladin calls attention (p. 209) to the general relation between rate of carbon dioxid elimination and the percentage of "indigestible" or "protoplasmic" proteins in various tissues. Such proteins are chiefly of the group known as nucleoproteins, and in the corn or wheat kernel are present largely in the germ. Such indirect evidence lends further support to the assumption that respiration in the endosperm cells of such grains is at a low level. Kolkwitz (1901) found that when he cut wheat kernels half way from end to end, the germ end respired three times as much carbon dioxid as the opposite end when equal weights of material were compared. Osterhout's (1917) observation that oxidation is more rapid in the nucleus than in the cytoplasm of living cells might also lead to the deduction that, since the cells of the germ have a larger proportion of nuclear material by weight than the large starchy parenchyma cells of the endosperm, respiration should proceed at a higher rate in the germ tissues.

There is reason for doubt, however, as to how much the various organisms such as bacteria and molds on the surface of the kernels contribute to the total carbon dioxid respired and heat energy released in bulk grain. Loew (1899) maintained that in the fermentation and heating of leaf tobacco the rise of temperature was due to the release of heat energy through the activity of the cellular oxidizing enzyms of the tobacco leaf tissues. He did not concede that microbial flora play any significant part in these heating processes, and opposed the bacterial-fermentation theory previously advanced by Suchsland (1891).

Nabokich (1903) sterilized beans with aqueous bromine (1 to 500) and corrosive sublimate (1 to 1000) solutions and then inoculated them with the washings from natural beans. The seeds so treated respired less carbon dioxid during the first day, but thereafter respired about one third more than the sterilized seeds which had not been inoculated. In a second series beans were sterilized and then inoculated with washings from a portion of the unsterilized seeds, with which their respiratory rate was then compared. In general the sterilized seeds behaved peculiarly, in that they respired more vigorously than the controls at the outset, but later failed to reach so high a rate. The disinfecting solutions apparently acted as narcotics in effecting an initial stimulation followed by a reduction in the respiratory rate. Because of this fact the data presented by Nabokich are somewhat difficult of interpretation, and suggest that the use of such disinfectants in respiration studies may give rise to abnormal conditions, and yield results of doubtful value. Moreover he was working with water-soaked seeds, while in commercial grain the moisture content is much below maximum imbibition, and the substratum to which the molds and bacteria are attached is not so well suited to active propagation and metabolism of those organisms as is soaked material.

Gore (1911) concluded that in self-heating, physiological processes are probably the first to operate, while Rahn (1910) states that the curve of the process of spontaneous heating of organic matter, including grain, would not in itself indicate whether the heat was produced by chemical or microbial causes. E. M. Bailey (1912) studied the ripening of bananas and indicates that bacterial activity is not responsible for the heat produced or for other changes occuring during the ripening of the fruit. The marked increase in liberation of carbon dioxide resulting from raising the temperature of wheat from 45° to 55° C., which was observed by Bailey and Gurjar (1918) suggests that possibly thermophylic bacteria were partly responsible for the relatively large quantity of carbon dioxid liberated at such high temperatures. Ordinarily the respiration of organs of higher plants is depressed on raising their temperature above 40° or 45° C.

In bulk grain the factor of significance, however, is the total quantity of heat energy released per unit of time, and since the reactions which give rise to carbon dioxid are exothermic, it is not of vital importance to determine whether the heat energy is released as the result of respiration within the tissues of the kernel, or in respiration or other exothermic reactions on the surface of the grain. In either event the heat energy becomes distributed throughout the bulk of grain and serves to raise its temperature if not immediately dissipated into the surrounding medium. Carbon dioxid liberated in respiration and related phenomena can be conveniently and accurately determined. In these studies of shelled corn, as in the previously published studies of stored wheat by Bailey and Gurjar (1918), the rate of respiration was determined and reported in terms of the quantity of carbon dioxid respired per unit of time and material. This method of study is convenient because of the ease and rapidity with which each sample can be examined, as well as the more exact control which can be effected in working with small quantities of grain.

It is recognized that a determination of the respiratory rate does not afford a simple means of computing the temperatures which the grain in question would attain under commercial conditions of storage. The writer has previously indicated (1917) that the actual change of temperature depends not alone upon the rate of respiration of the grain, but upon the size and shape of the bulk, the insulation afforded by the material of which the container or bin is constructed, the temperature of the surrounding medium (usually air), and the initial temperature of the grain itself. An equation by means of which the temperature change can be computed is accordingly complex, involving several variables, but such an equation has been presented and discussed by Hoffman (1918). Determinations of the rate of respiration are useful in comparing different lots of grain under uniform conditions of storage, however, thus affording a means for computing the relative quantity of heat evolved under the conditions imposed. This can not be done with large quantities of grain, since in such cases anything approaching an exact control of the physical conditions of the environment is manifestly unattainable.

METHOD OF STUDYING GRAIN RESPIRATION

In determining the rate of respiration the first step was to seal a suitable quantity of corn in a large calcium chloride tower. The weight of corn used depended upon the moisture content. When this was under 14 per cent it was customary to use from 500 to 800 grams of grain, while the weight used was reduced as the moisture content increased until only from 100 to 150 grams were employed when the moisture content was in excess of 17 per cent. The quantity of respired carbon dioxid could thus be kept within the limits of capacity of the absorption vessel. At the time of sealing the grain in the tower a representative sample was drawn for analysis. Air in the tower was drawn off and replaced by air freed from carbon dioxid, after which all joints were carefully sealed with paraffin. In all instances except when temperature was the variable (one series), the cylinders of grain were maintained at a temperature of 37.8° C. (100° F.) in an air thermostat. This temperature was maintained because the experience of the trade, as well as observations made in controlled experiments, indicates that at or slightly above 100° F. the condition known as "bin-burn" or "heat-damage" makes its appearance. The behavior of grain at this temperature is of particular interest, since it determines whether its temperature will continue to rise until serious damage results to the grain, or whether the heat energy released in bulk grain will be dissipated into the surrounding atmosphere as fast as produced in respiration. Acceleration of respiration with increasing moisture content was determined in one series incubated at 27.8° C., or 10 degrees lower than the temperature employed in all the other series. There was no significant difference in the response to increasing moisture content in the series at 27.8° C., the respiratory rate being a fairly constant fraction of the rates observed at the higher temperature.

The grain was allowed to respire about 96 hours before drawing off the carbon dioxid, because it appeared from preliminary studies that sufficient carbon dioxid to depress the respiratory rate did not appear in that time. Extending the period appreciably would, in the case of damp corn, result in a reduction of the rate of respiration. Shortening the period was not deemed advisable because (1) the quantity of carbon dioxid respired by dry grain would have been reduced to so small a quantity as to be difficult of accurate determination, and (2) the time required to heat the grain from its initial temperature (that of the laboratory atmosphere) to the temperature of the thermostat would have constituted too large a proportion of the total period of respiration, thus increasing the error from that cause. Since it was not always convenient to incubate for exactly 96 hours, the time that the towers were in the thermostat was noted, and the results were

calculated uniformly to a 24-hour basis. Continuous removal of the respired carbon dioxid by aspiration during the entire incubation period was suggested, but proved unfeasible because such treatment altered the moisture content of the grain.
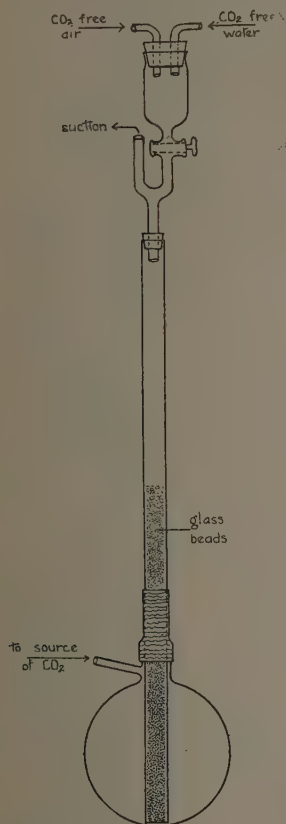
Figure 1. Modified Truog Absorption Tower

Immediately after the towers containing the corn were removed from the thermostat they were connected through an outlet tube to the absorption device. The latter was a tower similar to that described by Truog (1915), but slightly modified by using a round-bottomed distilling flask in place of a suction flask, and by providing a small reservoir for distilled water over the tower tube. The round-bottomed distilling flask is of the style furnished with the Brown-Duvel moisture-testing apparatus, and is convenient for a number of reasons. The round bottom is of advantage because more of the alkaline solution that is used can be drawn up into the tower tube than is possible with the ordinary suction flask. The straight sides of the neck of the distilling flask make possible the selection of a tower tube which fits quite snugly within the neck, and is of so nearly the same external diameter as the latter that a tight joint can be produced by slipping a piece of gum "gooch tubing" over both neck and tube at the point where the latter emerges. Thick-walled distilling flasks of the style mentioned can be purchased which are sufficiently substantial to give excellent service. The complete absorption tower is illustrated in Figure 1.

In the tube of this tower was placed a measured volume of nearly saturated barium hydroxid solution, the volume used being varied somewhat, depending upon the quantity of carbon dioxid to be absorbed. With dry corn 20 cc. of the barium hydroxid solution was used, while with damp grain this was increased to 50 cc. The calcium chlorid towers in which the grain was contained were provided with inlet tubes at the top through which carbon-dioxide-free air could be admitted, while the air containing respired carbon dioxid was drawn off through a tubulure at the bottom and passed into the absorption

tower containing the $Ba(OH)_2$ solution. Ten volumes of air were thus drawn down through the grain, completely sweeping out the carbon dioxid. When the carbon dioxid had been removed and absorbed, the residual $Ba(OH)^2$ in the absorption tower was determined by titration with standard HCl solution, and since the original charge of $Ba(OH)_2$ was known, a simple calculation gave the quantity converted into carbonate, which in turn could be computed in terms of carbon dioxid.

The Cain-Maxwell (1919) method for the determination of carbon dioxid was also employed in the later stages of these studies. The principle involved in this method is the measurement of the rise of electrolytic resistance of a solution of $Ba(OH)_2$ by its conversion into $BaCO_3$ as CO_2 is absorbed. A special combined conductivity cell and absorption vessel was devised by Cain and Maxwell which allows the ready and complete absorption of CO_2 in passing through the barium hydroxid solution and the measurement of the electrolytic resistance of the solution before and after the absorption of the carbon dioxid. Through the use of formulas or charts the change in resistance can be converted into terms of CO_2. The cell and absorption vessel are illustrated in Figure 2.
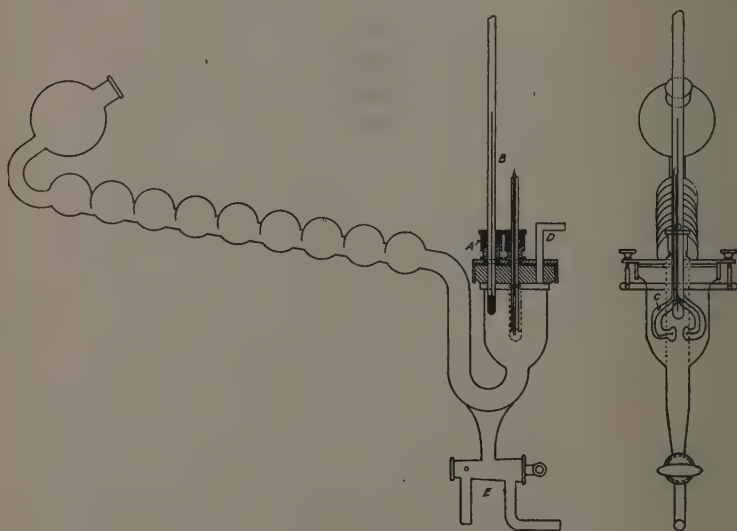
Figure 2.   Cain-Maxwell Cell and Absorption Vessel

An aqueous solution of about 7.2 grams of $Ba(OH)_2$ per liter is prepared and exactly 200 cc. of this solution are admitted into the cell through the three-way cock in the base. The cell is provided with a graduation showing the height to which this quantity of solution rises.

The temperature of the solution in the cell is observed, and the electrolytic resistance is measured by means of the conventional Wheatstone bridge set-up, using a telephone receiver or a high-sensitivity, alternating-current galvanometer to detect the point of balance. A simplified resistance-measuring device is available which embraces a set of resistances connected to dials arranged in decades, and a galvanometer which is operated on the ordinary 110-volt, 60-cycle, alternating current. This device does away with telephones, high frequency generators, balanced inductances and capacities, and relieves the operator of the strain and consequent fatigue attendant upon the use of such instruments.

Mixtures of air and carbon dioxid are aspirated through the Cain-Maxwell cell and absorption vessel at a rate not to exceed from 300 to 400 cc. per minute. To determine at any time the quantity of carbon dioxid absorbed, the current of gases is shut off, the solution allowed to flow back into the cell, its temperature observed, and the electrolytic resistance measured as before. These data can then be converted into terms of carbon dioxid through the use of appropriate formulas or the nomograph prepared by Cain and Maxwell. This nomograph makes possible the application of the temperature correction in a simple manner. Since the nomograph as furnished with the cell has an arbitrary "carbon scale" rather than a scale in terms of carbon dioxid, the latter is calculated, each small unit representing 0.01 per cent on the carbon scale of the nomograph being equivalent to 0.733 milligrams of carbon dioxid.

Barium hydroxid solutions containing less than 5.5 grams of $Ba(OH)_2$ per liter of solution are not very efficient in absorbing carbon dioxid unless the gases are bubbled through it at a slow rate. It is therefore advisable to cease aspirating through a cell which has a cell constant of 0.715 when the resistance of its contents exceeds 110 ohms, this being the resistance at 25° C. which is equivalent to about a safe minimum concentration of $Ba(OH)_2$. If the initial concentration of $Ba(OH)_2$ is 7.2 grams per liter, the cell has a capacity for about 80 milligrams of carbon dioxid. A more concentrated solution of barium hydroxid could be employed where larger quantities of carbon dioxid must be absorbed at one operation, it being possible at least to double the capacity of the cell, altho at the expense of accuracy. The nomograph prepared by Cain and Maxwell must be expanded in order to accommodate it to the use of more concentrated solutions.

Certain advantages of this method over the titrimetric procedure are: (1) No standard volumetric solutions are required. (2) The quantity of carbon dioxid respired during any interval of time can be determined without disconnecting or tearing down the set-up, by momentarily shutting off the gas stream and measuring the electrolytic

resistance of the solution. (3) Through the use of the simplified bridge and alternating current galvanometer, measurements can be made by a relatively inexperienced operator. The two outstanding objections which have been suggested are (1) the cost of the necessary equipment, and (2) its limited capacity for carbon dioxid. The latter is not a serious objection in many plant respiration studies.

DISTRIBUTION OF MOISTURE BETWEEN COB AND KERNELS

Earlier studies having established that the moisture content bears an important relation to respiration in stored grain, the moisture distribution in ear corn during the curing process is of some significance. A lot of Johnson County white dent corn, grown at the Maryland Agricultural Experiment Station in 1920, was employed in an experiment to determine the comparative rate of change in moisture content of cob and kernels while curing. This corn was cut and shocked about October 21, 1920, and the ears were removed from the stalks and husked on October 28. One portion of this husked corn was hung up in the heated laboratory, while another portion was stored in an unheated barn. Moisture content of the cob and kernels of these two portions on different dates is shown in Table I, the same data being presented graphically in Figure 3. These show that as the ear dries out, the cob, which has a materially higher initial moisture content than the kernels, loses moisture at a more rapid rate; in this experiment containing less moisture than the kernels when the latter had a moisture content below 14 per cent.
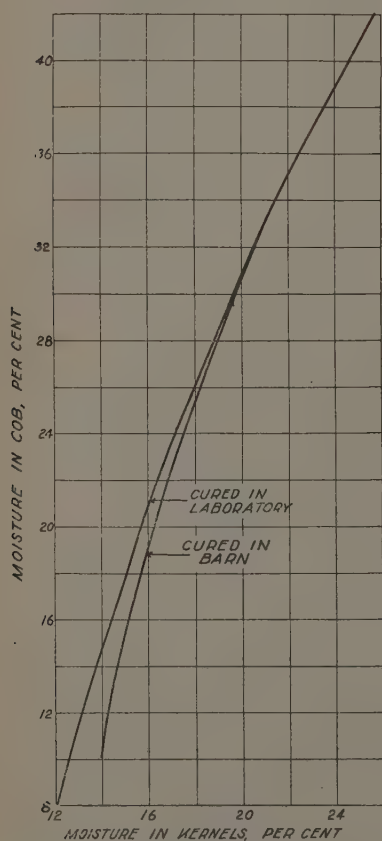
Figure 3. Percentage of Moisture in Cob and Kernels During Curing of Ear Corn

PERCENTAGES OF MOISTURE IN COB AND KERNELS OF EAR CORN AT DIFFERENT TIMES DURING CURING PROCESS

	Moisture content			
Date	Cured in laboratory		Cured in unheated barn	
	Cob	Kernels	Cob	Kernels
1920	Per cent	Per cent	Per cent	Per cent
Oct. 28*...............	42.02	25.77	42.02	25.77
Nov. 4.................	26.00	17.80	....	....
Nov. 12................	13.78	14.41	32.07	20.69
Nov. 24................	....	....	26.31	18.37
Nov. 29................	8.06	12.05	....	....
Dec. 3.................	....	....	24.90	17.90
Dec. 24................	....	....	22.79	17.21
1921				
Jan. 15................	....	....	20.49	16.54
Feb. 16................	....	....	16.41	15.29
Mar. 18................	....	....	10.04	13.96

* Date husked.

HYGROSCOPIC MOISTURE IN SHELLED CORN

Shelled corn, like many other materials, is hygroscopic, and loses moisture to the atmosphere or gains moisture from it until the humidity of the latter is in equilibrium with the hygroscopic moisture of the grain. No data were found in the literature concerning the moisture content of shelled corn when in equilibrium with atmospheres of different relative humidity. A series of experiments was accordingly undertaken with a view to obtaining such data. Three samples of corn were used for this purpose: (1) Boone County white dent corn of the 1919 crop, supplied by the Office of Cereal Investigations, United States Department of Agriculture, and designated as Lab. No. B15; (2) Johnson County white dent corn of the 1920 crop grown at the Maryland Experiment Station, Lab. No. B32; (3) Sweet corn, Lab. No. B47, from the same source as B32. About 50 kernels of each of the three samples were spread out on pieces of paraffined wire gauze, and these suspended in the upper part of half-gallon museum jars. Five such jars were thus prepared, and the lower halves were filled with solutions of sulfuric acid in water, a different concentration being placed in each jar. These concentrations were so adjusted, using the Regnault tables,[2] that the resulting relative humidities of the atmospheres in the jars ranged between about 35 and 85 per cent at 25° C. The jars were placed in an incubator maintained at 25° C., and the grain remained exposed to the several atmospheres until no further change in weight took place. This required about three weeks, when the change in moisture content was considerable. The grain was then

[2] Landolt, Börnstein, Roth. Physikalish-Chemische Tabellen, 4 Auflage, p. 426. 1912.

removed and the percentage of moisture which it contained was determined; the specific gravity of the sulphuric acid solutions was also determined at the time the grain was removed, and the humidity data were reported on the basis of conditions prevailing at the close of the experiment rather than at the beginning.

The data resulting from these experiments are given in Table II, and represented graphically in Figure 4. These show consistent differences in the relative hygroscopicity of the three samples, with B32 the highest and B47 the lowest in that regard. Whether the fact that the latter was sweet corn has any bearing on its relative hygroscopicity is hardly determinable from the available data, but this seems probable from other considerations. The mean percentages of hygroscopic moisture in the three samples studied ranged from 8.25 per cent
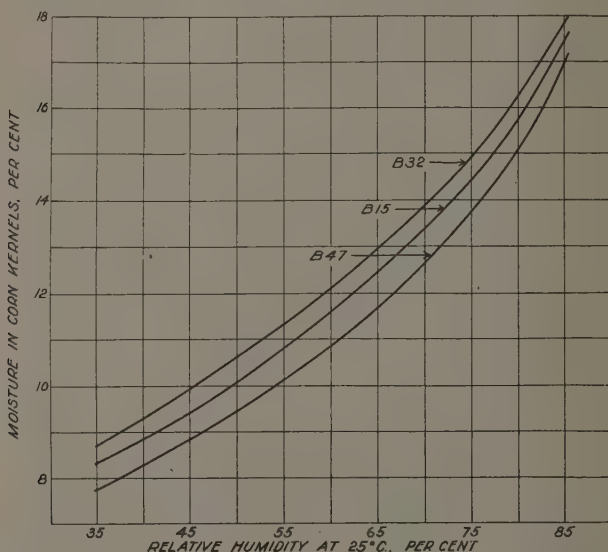
Figure 4. Hygroscopic Moisture in 1919 Crop Dent Corn (B 15), 1920 Crop Dent Corn (B 32), and 1920 Crop Sweet Corn (B 47), After Exposure to Atmospheres of Different Relative Humidity at 25° C.

at 34.8 per cent relative humidity (25° C.) to 17.57 per cent at 85.4 per cent relative humidity. It is thus evident that the percentage of moisture in corn may undergo considerable change when exposed to atmospheres of different humidity, providing the conditions of exposure are such that the movement of water vapor can take place. This depends, in turn, upon the size and shape of the parcel of grain, the material in which it is contained, the extent of air circulation, and other factors. It is probable that no considerable response to changes in

atmospheric humidity will be experienced in handling and storing bulk shelled corn, since the exposure is too slight. Surface layers might be affected, but to so slight a depth that it would represent only a small fraction of the total bulk. Ear corn in cribs can respond somewhat more readily to such changes, and seed corn hung up in seed houses will doubtless show an even greater response.

TABLE II

HYGROSCOPIC MOISTURE OF SHELLED CORN EXPOSED TO ATMOSPHERES OF DIFFERENT RELATIVE HUMIDITY AT 25° C.

Relative humidity of atmosphere at 25° C.	Hygroscopic moisture			
	B 15	B 32	B 47	Average
Per cent	Per cent	Per cent	Per cent	Per cent
34.8	8.32	8.69	7.73	8.25
54.1	10.62	11.18	10.04	10.61
71.3	13.66	14.31	12.96	13.64
78.7	15.23	15.80	14.10	15.04
85.4	17.61	17.95	17.15	17.57

DISTRIBUTION OF MOISTURE IN THE CORN KERNEL

Attention has been called by Babcock (1912) to the distribution of moisture in corn kernels which had been immersed in boiled water for 24 hours. Under such circumstances he found the embryo contained about 52 per cent of water, while the "starchy portion" contained about 32 per cent. In air-dried corn the embryo contained 5.62 per cent of moisture, the starchy portion 7.10 per cent.

TABLE III

DISTRIBUTION OF MOISTURE BETWEEN THE GERM AND THE DEGERMINATED RESIDUE OF WHITE DENT CORN

Moisture in		
Entire kernel	Germ	Degerminated residue
Per cent	Per cent	Per cent
13.39	10.05	13.47
14.32	11.25	14.51
15.11	12.32	15.35
16.94	15.51	17.12
19.17	21.73	18.85
21.77	26.83	21.15
24.50	36.25	23.04

In order to supplement these data by determining the distribution of moisture between germ and non-germ structures through the range of moisture content of commercial corn, several portions of the white
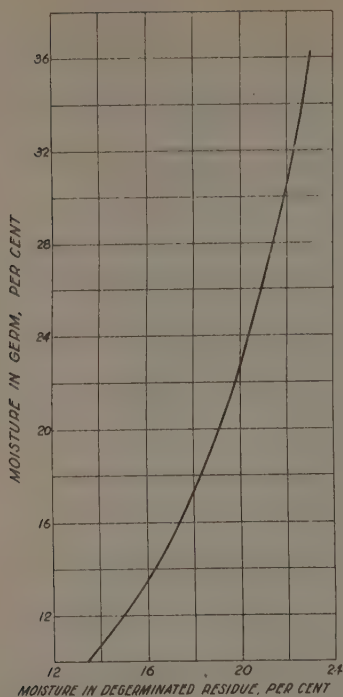
Figure 5. Percentage of Moisture in Germ, and Degerminated Residue of Corn Kernels

dent corn sample, B15, were each brought to a different moisture content by the addition of water. These were then placed in a refrigerator for four days to allow the distribution to proceed to completion. The germ, or embryo, was then dissected out with a small scalpel, and the moisture in the germ and the degerminated residue was determined. Table III and Figure 5 show the moisture content of the degenerated residue to have been higher than that of the embryo, with increasing moisture content until the kernel contained in excess of 18 per cent of moisture. From this point on, the germ contained more moisture than the residue until at the higher levels the ratio was about 1.5 to 1. It thus appears that in No. 3 corn containing somewhat more than 17.5 per cent of moisture, the percentage of moisture in the germ and in the residue of the kernel is approximately the same.

RELATION BETWEEN MOISTURE CONTENT AND RESPIRATION IN NORMAL CORN

Earlier investigations indicated that increasing the moisture content of seeds and tubers accelerated their rate of respiration. Lund (1894) made such an observation in the case of roots and tubers. Kolkwitz (1901) reported that barley kernels with from 10 to 11 per cent of moisture respired very feebly, liberating ⅓ to 1½ milligrams of carbon dioxid per kilo in 24 hours. On moistening them the intensity of respiration increased, with a "critical turning point" at 15 to 16 per cent of moisture. At 20 per cent of moisture respiration was much stronger, while at 33 per cent about 2000 milligrams of carbon dioxid were respired.

Qvam (1906) also observed an increased rate of respiration in barley as the percentage of moisture was increased.

White (1909) found that cereals respire appreciable quantities of carbon dioxid in an "air-dried" condition, while drying them for 8 days

at 45° C. depressed respiration to a level which resulted in quantities of respired carbon dioxid too small to be determined by the methods employed.

Duvel (1904), in studying the vitality of stored seeds, observed that the concentration of respired carbon dioxid in closed containers was increased with increasing percentages of moisture in the seed. At the same time there was a reduction in the percentage of viable seed.

Bailey (1917) reported observations of stored wheat in elevators at Duluth. Wheat containing 15.5 per cent of moisture was stored in an elevator bin September 11, 1914, and did not respire vigorously enough to raise its temperature above 72° F. during the succeeding fall months. Another lot of wheat containing 16.5 per cent of moisture, stored at the same time, was actively heating in 49 days, at which time it had reached a temperature of 80° F.

Experiments of Duvel and Duval (1919), to which reference has already been made, establish a correlation between moisture content and heat liberated as the result of respiration. One series of these investigations illustrates the effect of moisture content on rise of temperature. The corn in this experiment was loaded in box cars at Baltimore on April 14, 1910, and hauled to Chicago and back, and unloaded on May 11, 1910.

Car no.	Moisture in corn	Average temperature of corn when—	
		Loaded April 14	Unloaded May 11
	Per cent	°F.	°F.
1	19.8	58	139½
2	18.6	52	84
3	17.8	54	82½
4	17.4	54	58½
5	16.7	58	62

The difference between initial and final temperature in car No. 4 and car No. 5 is about the same, and suggests that the change in temperature in these instances may be attributed to heat absorbed from the atmosphere. Neither changed temperature significantly during the period of the experiment.

Bailey and Gurjar (1918) found that increasing the moisture content of wheat accelerated the rate of respiration. The relative increase in carbon dioxid respired per unit increase in moisture content is shown in Table V.

For the purposes of these corn-respiration studies, six samples of white and yellow dent seed corn grown in Texas, Arkansas, Missouri, Iowa, and Minnesota were secured, and one sample of white flint corn from North Dakota. These were reported by the experiment station

agronomists of the several states to be representative of the states in which they were produced. They accordingly represented wide extremes of dent corn types, from large-eared, late-maturing varieties of the south, to small, compact-eared, early-maturing varieties of the north. Any inherent differences in the respiratory activity of these different types should accordingly manifest themselves in the samples selected. To insure that no damaged kernels or foreign substances were present to affect the results, each sample was carefully screened and hand picked to remove such material. Germination tests showed the cleaned samples to be normally viable.

The laboratory numbers and a description of the samples are given in the following table:

Lab. No.	Variety	Color	Grown at	Crude protein (N X 6.25)	Wt. per 1000 kernels
				Per cent	Grams
6854	Minnesota No. 13	Yellow	St. Paul, Minn.	10.55	260
6855	White flint	White	Fargo, No. Dak.	11.31	288
6858	Tuxpan	White	Dallas, Texas	10.81	368
6859	Reid's Yellow Dent	Yellow	Ames, Iowa	10.62	400
6862	Reid's Yellow Dent	Yellow	Columbia, Mo.	9.75	342
6860	Commercial White	White	Columbia. Mo.	10.93	444
6861	Mexican June	White	Phoenix, Ariz.	11.18	336

Each sample was subdivided into eight or ten portions, and each portion was then brought to a different moisture content by the addition of water. The percentages of moisture thus ranged from the original moisture content of the air-dry corn (10.2 to 11.7 per cent) to about 18 per cent. These limits were imposed because it is within this range that respiration reaches a sufficiently high level under certain commercial conditions to raise the temperature of bulk grain to a point where damage will ensue. Duvel and Duval (1913), in a series of experiments with corn in box cars, found a carload containing 16.0 per cent of moisture and loaded on May 11, 1911, to be actively heating on June 3, 1911, with a temperature of 100.2° F. Shanahan, Boerner, and Leighty (1910) report entire holds of corn shipped in vessels from America, containing as low as 15.6 per cent of moisture, to be in a heating or hot condition when examined in Europe (note, for example, cargo 170); while considerable percentages of certain holds were found in a heating or hot condition when the moisture content was under 15 per cent (note cargoes 127, 168, 169, and 172). The total percentage of American corn found heating or hot on arrival in Europe during the three seasons from 1905 to 1908 was as follows (from Shanahan, Boerner, and Leighty's paper).

Moisture content Per cent	Heating or hot on arrival Per cent
12.1 to 14 .	6.6
14.1 to 16	7.7
16.1 to 18	14.9
18.1 to 20.6	12.8[8]

[8] The fact that this percentage is lower than for corn containing from 16.1 to 18 per cent of moisture was due to favorable shipping conditions.

Boerner (1919) studied several cargoes of American corn en route to European ports, and found in certain instances that corn containing less than 18 per cent of moisture was hot or heating near the surface on arrival at the port of destination. Seasonal conditions, proximity to engine-room bulkheads, and access to air, functioned with moisture content in determining the rate and extent of heating.

Several samples of heating corn which contained less than 17 per cent of moisture were supplied for these studies by the Minneapolis laboratory of the Office of Federal Grain Supervision. These were drawn from car lots inspected during the last half of June and the first week of July, 1920. From these considerations it appears that corn containing less than 18 per cent of moisture is likely to heat when handled in bulk, and that data establishing the comparative respiratory rate between that limit and that of dry corn will be of the most service at this time.

In conducting these studies, triplicate determinations of the rate of respiration of each portion of the several corn samples were made at a temperature of 37.8° C. (100° F.). Approximately two hundred determinations are accordingly included in the studies of the seven seed-corn samples. The averages of these determinations are given in Tables XVII to XXIII in the appendix. Graphs were drawn for each of the seven samples, and from these the rates of respiration at even percentages of moisture from 11 to 18 per cent were computed by interpolation. The samples were then classified into "northern" and "southern" groups, those grown in North Dakota, Minnesota, and Iowa being included in the first group, while those grown south of Iowa constituted the second group. The average rate of respiration of the corn in the two groups was then calculated. It appears from these data, which are given in Table IV and shown graphically in Figure 6, that the corn samples in the northern group respired somewhat more vigorously than those in the southern group, altho the differences are not appreciable until the moisture content exceeds 15 per cent. Such a difference is perhaps to be anticipated, since early maturity in the northern-grown varieties may be correlated with a higher rate of respiration in the germinating seed, for rapid growth and development of the seedlings of early maturing varieties may possibly
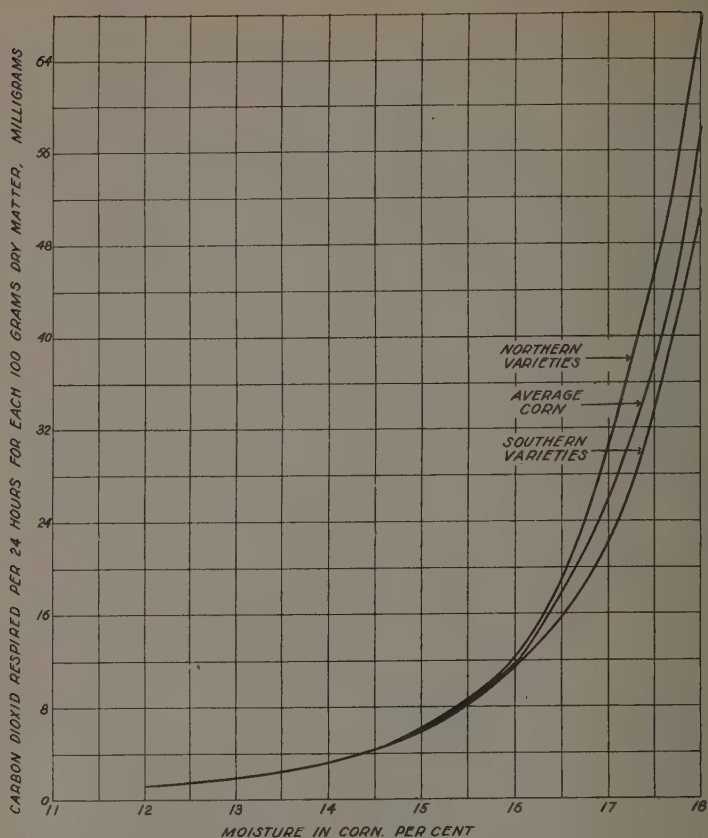
Figure 6. Respiration of Northern Varieties, Southern Varieties, and Average Corn

contribute to the relative rate of development. This is suggested by the work of Reed and Holland (1919), who state in the opening paragraph of their paper "If we assume that growth is a dynamic process and the organism is produced as its end-product, certain relations ought to exist between the size of the organism at any given time and the final size attained in time, T." They then present data in support of such an assumption and establish that growth rate of sunflower plants approximates closely the curve of an autocatalytic reaction. While their observations began with plants already 10 centimeters high, the writer believes it might properly be assumed that physiological responses which result in an early maturity of a plant would also be reflected in rate of germination of the seeds of that plant. If a higher germination rate is encountered in certain corn varieties than in others, this should be expected to be correlated with either (a) a higher concentration of

enzymes concerned with the progress of germination, or (b) a lower optimum temperature for such enzymes, resulting in more rapid hydrolytic and other enzymic reactions at the comparatively low temperatures frequently prevailing in the soil at the time of corn planting. The possibility of establishing such correlations has suggested itself, but must be reserved for later studies.

Differences observed in the respiratory rate of northern and southern grown corn varieties are hardly great enough to justify a classification on the basis of point of origin or variety in standardizing commercial corn with respect to keeping qualities.

TABLE IV

RATE OF RESPIRATION OF NORTHERN AND SOUTHERN CORN VARIETIES 'AT' EVEN PERCENTAGES OF MOISTURE

Moisture	Carbon dioxid respired per 24 hours for each 100 grams of dry matter		
	Northern varieties	Southern varieties	Average
Per cent	Mgm.	Mgm.	Mgm.
11	0.77	0.70	0.73
12	1.19	1.15	1.17
13	1.91	1.75	1.82
14	3.21	3.17	3.18
15	6.20	5.91	6.02
16	12.21	11.55	11.83
17	30.98	22.16	25.94
18	67.73	50.86	58.09

The acceleration of respiration with increasing moisture content was then calculated, and these data are given in Table V. In making these calculations the formula $\dfrac{K_m - K_{m-1}}{K_{m-1}}$ was employed, in which K_m represents the rate of respiration at any particular percentage of moisutre (m), and K_{m-1} the rate when the sample contained 1 per cent less of moisture $(m-1)$. The values thus represent the fractional increase in respiratory rate by intervals of 1 per cent change in moisture content. For example, the rate of respiration of average sound seed corn, as shown in Table V, was increased by 56 per cent when the moisture content was increased from 11 to 12 per cent.

It appears that the relative acceleration with increasing moisture is much more uniform than was found in the experiments with wheat previously reported by Bailey and Gurjar (1918). When the moisture content of sound spring wheat was increased, a sharp break in respiratory rate appeared between 14 and 15 per cent of moisture, while the relative acceleration increased further with progressive increases in moisture content above the latter figure. In the case of these corn samples no such sharp break in the curve appears, altho a uniform increase in relative acceleration with increasing moisture content is apparent from the data given in Table V.

TABLE V

ACCELERATION OF RATE OF RESPIRATION OF SOUND CORN AND SOUND SPRING WHEAT WITH INCREASING MOISTURE CONTENT

Cereal	Acceleration between the following percentages of moisture						
	11 to 12	12 to 13	13 to 14	14 to 15	15 to 16	16 to 17	17 to 18
Corn	0.56	0.60	0.75	0.89	0.97	1.19	1.24
Spring wheat.........	...	0.16	0.17	0.66	1.41	3.02	...

Reasons for such marked acceleration of respiration as result from comparatively small increases in moisture content are still within the realm of hypothesis. The author (1917) has previously suggested that these are to be found in part at least in the colloidal properties of the materials which chiefly constitute the kernel. When "dry," the limited hygroscopic water present is held by the colloids under high tension. Hales (1727), nearly two centuries ago, observed that germinating pea seeds would swell under a pressure equivalent to 83.5 kilos. Rodewald (1895) computed that dry starch imbibed water in swelling under a pressure of 2605 kilograms per square centimeter, or 2523 atmospheres. Materially higher values were assigned by Sachs (1882), and Patten (1907) suggests that Rodewald's value is too low. It has even been estimated that the pressure in such instances is sufficient to cause the imbibed water to possess certain properties of a solid. Increasing the moisture content diminishes the pressure under which each successive addition is held by the colloidal system. Thus Shull (1913) shows that in an air-dry Xanthium seed which contains from 8 to 9 per cent of hygroscopic moisture, the imbibition force is 965 atmospheres, and that the addition of 7 per cent more water reduces the imbibition force to 375 atmospheres. The possibility of diffusion of the water-soluble substances present must be progressively enhanced by successive additions of water to the kernel. This accelerated diffusibility would affect not alone the soluble solids, as sugars and mineral salts, but also gases, as oxygen and carbon dioxid. Respiration could hardly proceed unless the substances involved in the chemical reactions move, chiefly by diffusion, to the seat of respiration. If, as Osterhout (1917) postulates, oxidations proceed chiefly in the nucleus of the cell, a diffusion within the cell would be necessitated, if not from cell to cell and tissue to tissue. Certainly the gases involved must move through cells and tissues, particularly in aerobic respiration.

Bearing on this hypothesis are the results of measurements made with the electrode designed by Zeleny (1909), modified somewhat so that the two metal points of copper and zinc respectively are mounted
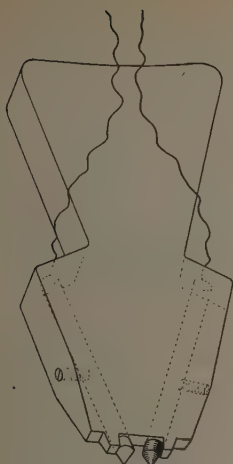
Figure 7.   Modified Zeleny Electrode

in a vulcanite handle and with the axes of their points parallel to each other. The modified electrode is shown in Figure 7. These two points of dissimilar metal are pressed into the germ of the corn kernel, and the system Cu—Germ—Zn thus constitutes a small voltaic cell. The current flowing through this cell is a function of the percentage of moisture in the germ. This was observed by Zeleny, and confirmed by tests made in these studies. A composite sample of No. 2 mixed corn was divided into seven portions, each of which was brought to a different percentage of moisture, ranging from 13.89 per cent to 17.70 per cent, by the addition of varying quantities of water. These portions were then allowed to stand for several days in order to allow the distribution of water in the kernels to proceed to completion. The points of the Zeleny electrode were thrust into the embryos of corn kernels taken from each lot, and the deflections of a d'Arsonval galvanometer were noted when connected to this cell. The electrode points were forced into the germs under a uniform pressure maintained by a simple mechanism consisting of a lever and coiled spring. More uniform results could be obtained in this manner than when the electrode handle was held in the hand in introducing the points. Average deflections of each of the seven lots, together with the moisture content, are given in Table VI and shown graphically in Figure 8. During several preliminary tests it developed that the deflections resulting from measurements made with different kernels taken from the same sample, and presumably having the same moisture content, varied widely when the kernels tested were of varying size and structure. Size of the germ in particular seemed to affect the galvanometer deflections. In the series reported in Table VI, those kernels differing materially from the average in shape and size of germ were rejected, and tests were made only of those approaching the average in these regards.

The cells did not give the maximum reading with the galvanometer immediately upon inserting the metallic points into the corn embryos. About 30 seconds were usually required for the galvanometer coil to deflect to the maximum, after which it gradually rotated back to its original position, indicating a polarization of the cell. Maximum deflections observed were recorded in each instance.

Electrical potentials of these cells were also determined, by connecting the wire leads from the electrodes to the E. M. F. connectors

of a Leeds and Northrup Type K potentiometer. While this instrument is probably not well adapted to the measurement of potential from such sources, it was evident that changes in potential on increasing the moisture content of the grain were of small magnitude compared with the changes in galvanometer deflections. The latter being a function of current, it is evident that the current flowing through such a cell is low when dry corn germs are tested, while the current increases decidedly on raising the moisture content, indicating a comparatively enormous decrease in the electrolytic resistance of the cell, the E. M. F. of which is fairly constant.
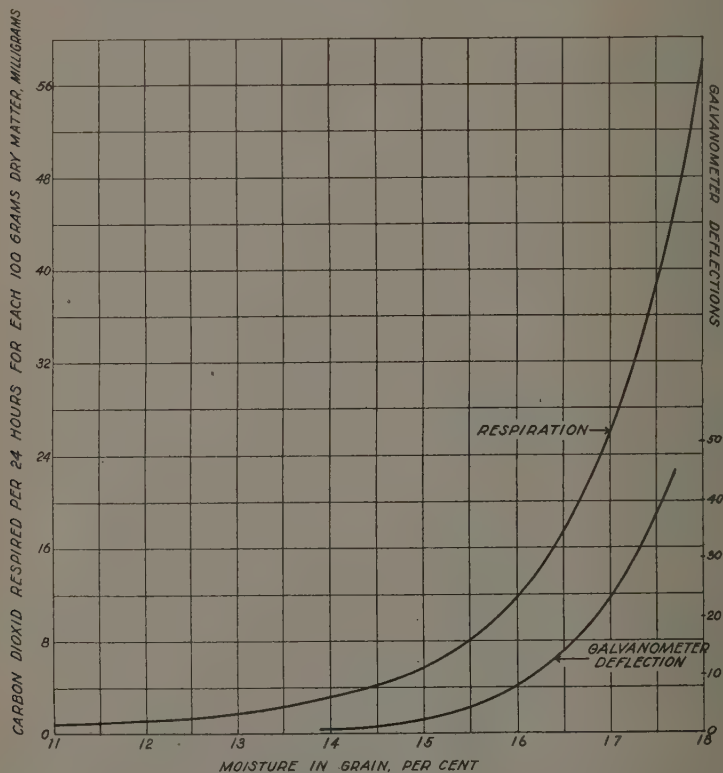
Figure 8. Comparison of Rate of Respiration of Corn, and Galvanometer Deflections with the Zeleny Electrode

Resemblance of the curve in which galvanometer deflections are plotted against moisture content, to the curve in which respired carbon dioxid is plotted against moisture content, shown in Figure 8, suggests that the same phenomena are operative in determining electrolytic resistance of the corn germ and respiratory activity of normal grain. Resistance encountered by ions in moving between the poles of the

electrode is probably responsible in large part for the high electrolytic resistance of dry corn germs, while the hypothesis is advanced that resistance to the free movement of ions and molecules through the same material may likewise be responsible for reduced respiration in dry grain.   The relation of the limited quantity of water present to the colloids of the grain is believed to determine the comparative rate of movement of dissolved solids and gases in the system.

TABLE VI

POTENTIALS AND GALVANOMETER DEFLECTIONS RESULTING FROM THE INSERTION OF THE CU-ZN
ELECTRODE INTO GERMS OF KERNELS OF VARYING MOISTURE CONTENT

Sample	Moisture	Galvanometer deflection with Cu-Zn electrode
46b	13.89	0.7
46c	14.52	1.7
46g	15.16	3.5
46d	16.00	7.7
46e	16.51	14.2
46h	17.23	29.9
46f	17.70	45.0

RESPIRATION OF CORN DURING THE CURING PROCESS

In Table I it was shown that the moisture content of a lot of white dent corn diminished during the curing process.   The respiratory activity of the same lot of corn was determined at intervals while curing.   The results are shown in Table VII, together with the inter-polated rate of respiration of sound corn containing the same per-centage of moisture six months or more after harvest.   Unfortunately only one sample of the corn stored in the barn was subjected to a test of respiratory activity, this work being incidental to the other studies, and no provision having been made for sufficient material to carry out an extended series.   It appears from the limited data available that the rate of respiration is lower in freshly harvested corn than in corn of the same moisture content several months after harvest.   The greatest relative difference was encountered in the corn which was shelled on November 4, 1920, from ears curing in the laboratory.   In this sample the rate of respiration was only about one-fourth that of normal corn a few months after harvest.   A sample of corn in the barn taken on December 3, 1920, or one month later, which contained nearly the same percentage of moisture, namely 17.9 per cent, respired 19 milligrams of carbon dioxid, or nearly twice as much as that shelled from the laboratory-cured sample on November 4.

It appears that a condition similar to dormancy may be involved in these reduced rates of respiration which corn exhibited in the first few weeks following harvest.   Crocker (1916), in summarizing the

factors contributing to dormancy of seeds, states that in certain species this may be due to inhibition or retardation of the passage of gases to or from the embryo by the testa, resulting in an accumulation of carbon dioxid within the tissues of the embryo or an insufficient supply of oxygen for germination. While corn kernels are not dormant in the sense usually implied by that term, and will germinate shortly after harvest, there might nevertheless be a reduced permeability to the gases involved in respiration. At any rate this seems the most logical explanation of the reduced rate of respiration observed in the grain when first harvested. It is probable that after a period of from four to six weeks the conduct of the grain in this regard rapidly approaches the normal for ripened and cured corn. Reduced respiratory activity early in the curing process is fortunate and of advantage in that the liability of damage resulting from excessive respiration during the critical period when the moisture content of the grain is high, is thus diminished.

TABLE VII

RESPIRATION OF CORN DURING PROCESS OF CURING COMPARED WITH CORN OF THE SAME MOISTURE CONTENT SIX MONTHS OR MORE AFTER HARVEST

		Corn cured in laboratory	
Date sampled	Moisture in grain	CO_2 respired per 100 grams dry matter in each 24 hours	CO_2 respired per 100 grams dry matter in each 24 hours by corn of same moisture content 6 months after harvest
1920	Per cent	Milligrams	Milligrams
October 28.............	25.77	116.09	....
November 4............	17.80	10.97	46.70
November 12...........	14.41	2.18	4.07
November 29...........	12.05	1.24	1.20
		Corn cured in barn	
December 3............	17.90	19.00	47.00

After the period of reduced respiration there appears to be no material change in the respiratory rate of sound grain with further lapse of time during the remainder of the season, except such as accompanies desiccation of the grain. This is indicated by the results of an examination of several samples of the 1919 corn crop drawn from car lots of commercial corn by the Office of Federal Grain Supervision, at Minneapolis, during June and July, 1920. Cars that were sound and cool on arrival respired at about the same rate as the average seed-corn samples (Table IV) when the moisture content of the latter was increased by additions of water and the respiratory rate determined

three days later. The moisture content, grade, and rate of respiration
of these commercial lots of corn are shown in Table VIII.

TABLE VIII

RESPIRATION OF SOUND COOL COMMERCIAL DENT CORN OF THE 1919 CROP SAMPLED AT
MINNEAPOLIS DURING THE SUMMER OF 1920

Sample mark	Date sampled	Grade	Moisture	Wt. per bushel	Carbon dioxid respired per 24 hours by each 100 grams dry matter
	1920		Per cent	Lbs.	Milligrams
7706	June 17	3 yellow	15.6	56.2	8.52
7956	June 30	2 mixed	15.3	55.5	10.26
7959	June 30	3 yellow	15.8	54.3	12.03
6	July 1	6 white	15.1	56.2	7.55
9	July 1	3 mixed	15.2	55.8	7.02
112	July 7	2 mixed	15.0	56.8	7.70

EFFECT OF "FOREIGN MATERIAL AND CRACKED CORN" ON RATE OF RESPIRATION

In the federal standards for corn appear maximum limits of foreign
material and cracked corn which may be present in each of the six
numerical grades. Less is allowed in the higher grades, the limit pro-
gressively increasing from No. 1 to No. 6 corn. In grading corn this
material is separated by sifting the corn on a metal sieve perforated
with round holes 14/64 of an inch in diameter. The trade appears
to be of the opinion that the keeping qualities of bulk shelled corn are
impaired by the presence of broken material. In order to ascertain
the effect of such material, a series of samples was obtained from the
Baltimore laboratory of the Office of Federal Grain Supervision, which
had been graded on the basis of their content of foreign material and
cracked corn. Five samples of No. 4 mixed corn were composited.
These contained from 4.2 to 5 per cent of foreign material and cracked
corn, with an average of 4.7 per cent. A like number of sample grade
mixed corn samples were composited which contained from 7.4 to 10
per cent of foreign material and cracked corn, with an average of 8.7
per cent. The composite samples were practically alike in other par-
ticulars as is evident from the data in Table IX.

TABLE IX

CHARACTERISTICS OF THE NO. 4 MIXED AND SAMPLE GRADE MIXED CORN COMPOSITE SAMPLES
USED IN RESPIRATION STUDIES

Grade	Moisture	Wt. per bushel	Damaged kernels		Foreign material and cracked corn
			Total	Heat damage	
	Per cent	Lbs.	Per cent	Per cent	Per cent
No. 4 mixed........	12.9	56.0	2.8	0.0	4.7
Sample grade mixed.	13.1	56.5	2.4	0.0	8.7

These composite samples were each divided into four portions, and each of these was in turn brought to a different moisture content by the addition of water. After three days the rate of respiration was determined in the usual manner, with the results shown in Table X, and graphically in Figure 9. The latter also includes a portion of the curve for sound, clean seed corn (Figure 6), and indicates that foreign material and cracked corn appreciably accelerate respiration of the bulk at all percentages of moisture within the range studied. Injury of certain vegetative structures has been observed by other investigators to increase their rate of respiration. It is doubtful if in material where respiration is at so low a level as in these corn samples the mechanical injury has, in itself, any pronounced effect on respiration. More probably the improved conditions for gaseous diffusion to and from the respiring cells which result from cracking or crushing the kernel are responsible for part of the increased respiration. Improved opportunity for the growth of fungi of various sorts on the broken fragment, particularly when damp, may contribute also to the totality of respiratory phenomena. Whatever the actual cause, there is evidently a greater hazard in handling corn containing an appreciable quantity of cracked corn than in handling sound clean grain under similar conditions.
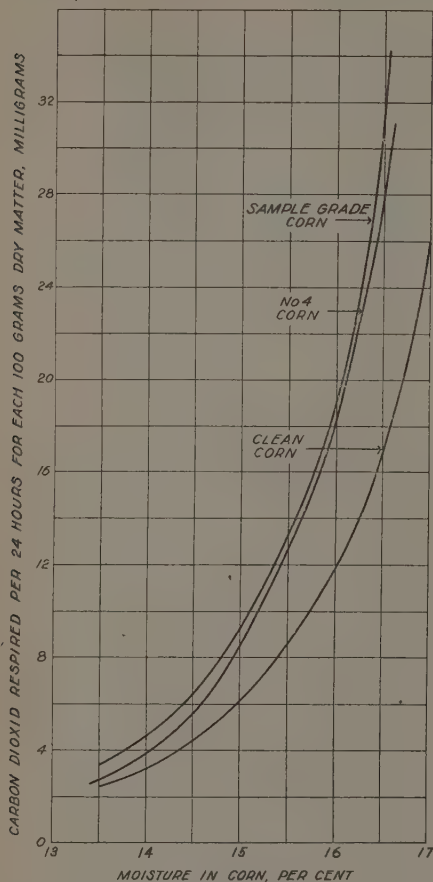
Figure 9. Effects of Foreign Material and Cracked Corn on Rate of Respiration

TABLE X

Respiration of Samples Containing Foreign Material and Cracked Corn

No. 4 mixed corn with 4.7 per cent of foreign material and cracked corn		Sample grade mixed corn with 8.7 per cent of foreign material and cracked corn	
Moisture	Carbon dioxid respired in 24 hours for each 100 grams dry matter	Moisture	Carbon dioxid respired per 24 hours for each 100 grams dry matter
Per cent	Milligrams	Per cent	Milligrams
13.40	2.56	13.50	3.35
14.63	6.14	14.97	9.16
15.62	13.83	15.68	15.02
16.67	31.14	16.56	34.28

RESPIRATION OF SPROUTED CORN

Bailey and Gurjar (1920) found that sprouted wheat kernels that had been dried until their moisture content was between 12 and 16 per cent respired more vigorously than sound wheat of the same moisture content. Within certain limits the length of time that germination of the grain proceeded appeared to be a function of respiratory rate. Thus wheat germinated for forty-eight hours and then dried respired at a higher rate than another portion of the same wheat sample which had been allowed to germinate for only twenty-four hours. Similar results were obtained in this study of corn. The seed laboratory of the Maryland experiment station germinated two portions of Boone County white dent corn (Lab. No. B15) in the manner usual to the testing of seed corn for three and five days. After drying the germinated kernels to a moisture content of about 11 per cent, each of the samples was subdivided into six portions, to which varying quantities of water were added. The rate of respiration of these was determined after a lapse of three days. Table XI shows the carbon dioxid respired by each of these portions, as well as by normal or ungerminated corn of the same original sample containing different percentages of moisture. The same data presented graphically in Figure 10 indicate that within the limits of moisture content studied, the germinated corn respired at a considerably higher rate than the ungerminated corn of the same moisture content. Sprouted or germinated corn would accordingly tend toward heating more readily when stored than sound corn of the same moisture content.

In the studies of germinated wheat already referred to, it developed that the ratio of respiratory rate in the several samples was not far different from the ratio of their reducing sugar content. This suggested that possibly accelerated respiration of sprouted grain might result from an increased concentration of those simple hexose sugars which are generally believed to constitute the principal substrate for

the enzyms concerned with respiration. It seems improbable that so simple an explanation will suffice. Doubtless more factors are operative than the mere concentration of reducing sugars. The colloidal condition of the hydrophyllic colloids in the damaged grain may conceivably play an important part in the altered respiration. Certain of these colloidal substances are known to undergo significant changes during germination, which involve progressive transformations to noncolloidal or crystalline compounds. Their water-imbibing capacity must be modified and reduced at the same time, and diffusion facilitated in the tissues of which they constitute an important part. The actual concentration of certain enzyms also apparently increases during germination, and possibly those enzyms involved in respiration may similarly increase.
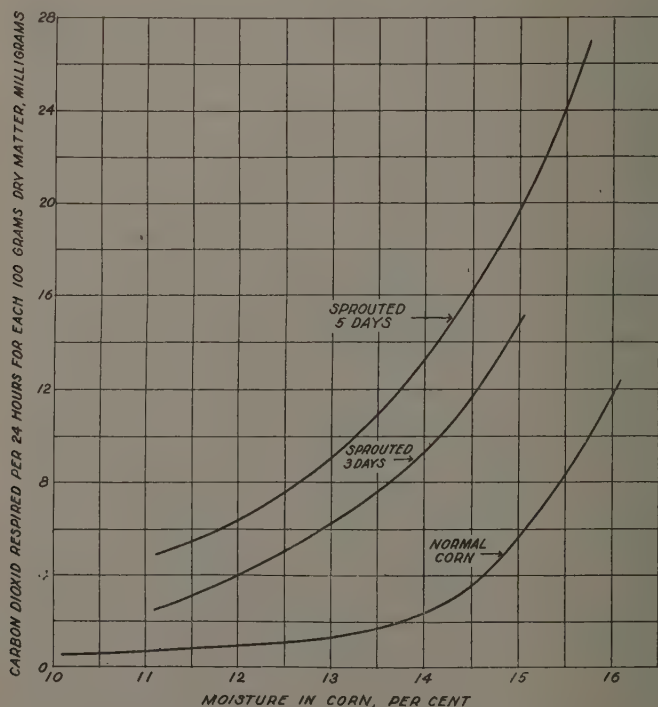
Figure 10. Respiration of Normal and Sprouted Corn Kernels

TABLE XI
RESPIRATION OF NORMAL AND GERMINATED BOONE COUNTY WHITE DENT CORN

Normal or ungerminated corn	
Moisture	Carbon dioxid respired per 24 hours for each 100 grams dry matter
Per cent	Milligrams
10.09	0.55
13.39	1.68
14.32	2.91
14.64	2.96
15.11	6.27
15.72	9.67
16.09	12.38
Kernels germinated 3 days	
11.09	2.51
12.38	4.76
12.84	6.03
13.19	6.61
14.30	10.61
15.03	15.04
Kernels germinated 5 days	
11.12	4.96
12.60	7.79
13.70	11.66
13.87	13.11
14.80	18.10
15.77	27.02

RESPIRATION OF HEAT DAMAGED CORN

It was developed in the opening paragraphs of this paper that heating corn will frequently reach comparatively high temperatures, occasionally as high as 65° C. (149° F.). The trade has noted, and controlled experiments have confirmed the opinion, that if the temperature exceeds 37.8° C. (100° F.) the kernels become discolored, while if the temperature continues to rise the kernels in time become "mahogany" or dark brown in color throughout. Such grains possess a peculiar characteristic odor, and a friable texture. The kernels generally fail to germinate when the damage is at all considerable. Besley and Baston (1914) described a method for determining the acidity of corn, and established a correlation between the comparative acidity (by titration) and the soundness of various corn samples. While forms of unsoundness other than heat damage are involved in instances of increased acidity, they indicate that when heating of sound corn occurs, the acidity increases. This is shown by the acidity (stated in terms of the number of cubic centimeters of one-hundredth normal alkali required to neutralize the acid in 10 grams of corn) of samples taken at different stages of marketing, in the following table (Besley and Baston, p. 11):

Kind of corn	Acidity	
	Average	Range
	c.c.	c.c.
Corn selected for seed............................	17.2	13.6 to 23.8
Country elevator receipts and shipments............	19.4	14.5 to 50.8
Terminal market receipts........................	20.4	11.7 to 66.4
Loaded at seaboard for export.....................	20.2	12.4 to 32.0
Discharged at foreign ports......................	30.4	16.0 to 110.8

They examined a cargo of corn with an initial temperature of 59° F., and an acidity of 20.4 cc., that when discharged at a European port had a temperature of 96° F., and an acidity of 29.8 cc. In nine cargoes the acidity of the corn when discharged varied directly with the temperature at that time. When the temperature was below 50° F. the acidity was 21 cc., while cargoes with a temperature above 100° F. at the time of discharge had an average acidity of 42.5 cc. Separations of sound and damaged kernels in approximately 3000 samples were made during parts of three seasons, and in these they found the following degrees of acidity (Besley and Baston, p. 40):

Degree of acidity

Sound kernels... 19.5
Broken kernels.. 22.5
Damaged kernels, exclusive of heat damage................... 41.2
Slightly heat-damaged kernels............................... 41.8
Badly heat-damaged kernels................................. 50.8

A graph included in their paper shows the acidity of the germ of damaged corn to be materially greater than that of the degerminated residue. Thus in No. 4 and sample-grade corn the degree of acidity of the degerminated kernels was about 18 cc., while for the germs of the same kernels it was about 90 cc. The source of titrable acidity is thus apparently in the germ.

Hydrogen ion concentration of certain typical sound and damaged corn samples used by the writer in these respiration studies was determined, and it was found to be generally higher in the damaged grain. This is shown by the data in Table XII. Sound corn samples possessed a lower hydrogen ion concentration than pH 6.2 ($[H]^+ = 0.62 \times 10^{-6}$), while the damaged corn samples were on the acid side of pH 6. ($[H]^+ = 0.99 \times 10^{-6}$). These are not wide differences, considering the badly damaged condition of such material as is represented by samples B1 and B2, and because of this fact the electrometric determination of hydrogen ion concentration is of limited value in determining the extent of damage represented in such material.

Since the work of Besley and Baston established that acidity increased chiefly in the germ or embryo of the kernel when the latter became damaged, a study was made of the hydrogen ion concentration of germ and degerminated portions of sound and damaged corn.

TABLE XII

Hydrogen Ion Concentration of Sound and Damaged Corn

	Sound corn	
Lab. No.	Description	pH
B 15	Boone County white dent seed corn................	6.29
B 11	No. 2 yellow corn from Baltimore................	6.37
B 13	No. 2 mixed corn from Baltimore................	6.24
	Damaged corn	
B 1	Damaged kernels, including heat-damage...........	5.95
B 2	Badly heat-damaged kernels....................	5.95
B 39	Sour and heating corn........................	5.65
B 15a	Same as B 15 after sprouting 5 days.............	5.72

Samples B15 and B39 were used for this purpose, with the results shown in Table XIII. From this it appears that the hydrogen ion concentration of sound corn germs may be decidedly less than the degerminated residue of the same kernels. The hydrogen ion concentration of damaged corn germs is somewhat higher than that of the degerminated residues of such kernels, but the difference is surprisingly small in view of Besley and Baston's findings. The small differences must be attributed to the high buffer action of germ extracts.

TABLE XIII

Hydrogen Ion Concentration of Germs and Degerminated Residues of Sound and Damaged Corn Kernels

Lab. no.	Description	Hydrogen ion concentration (as pH)		
		Whole kernels	Germ	Degerminated residue
B 15	White dent seed corn............	6.29	6.75	5.78
B 39	Sour and heating corn..........	5.65	5.48	5.65

In connection with these determinations of hydrogen ion concentration it was observed that the pH changed in the direction of increasing acidity with the lapse of time after grinding. Thus the pH of freshly ground meal from Lab. No. B11 was 6.37, while four months after grinding it was 5.41, a change of nearly one unit in terms of pH, or nearly ten times in terms of hydrogen ion concentration. Similar changes were observed in other samples, indicating that even with dry, sound material such determinations must be made immediately after grinding the corn.

Another observation of interest in this connection is that the ratio of meal to redistilled water in preparing extracts for electrometric hydrogen ion concentration determinations may apparently vary between

fairly wide limits without materially affecting the results. Ratios of meal to water of 1 to 5 and 1 to 10 resulted in small differences in the pH of the extracts.

Samples of hot and heating corn taken from box cars in the Minneapolis railroad yards by representatives of the Office of Federal Grain Supervision in the summer of 1920 were sent to the writer. These contained from 14.8 to 17.2 per cent of moisture. Their rate of respiration was determined, and these data are given in Table XIV. A comparison of these data with those shown for normal corn in Figure 11 indicate that these hot or heating lots of corn respired at a rate considerably above that of normal sound corn.
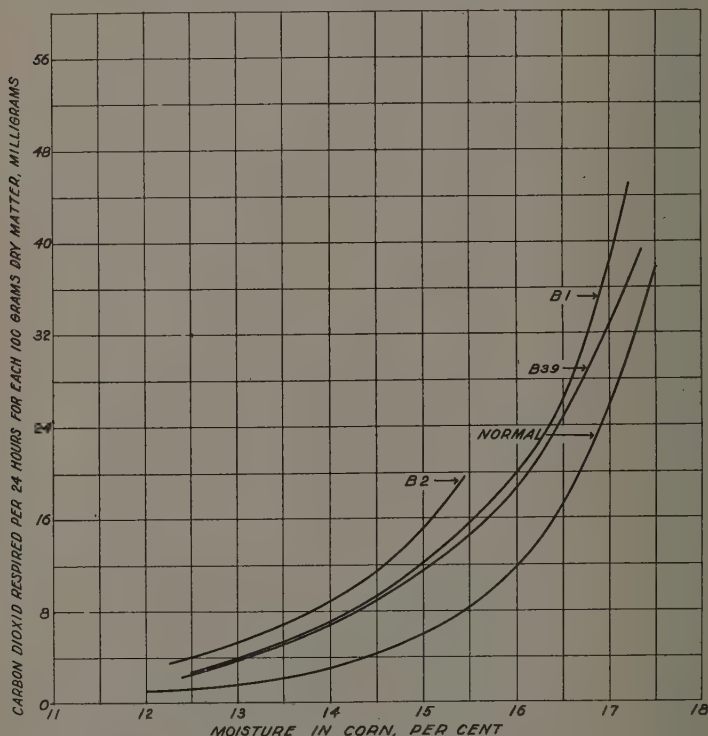
Figure 11. Comparative Respiration of Normal or Sound Corn, Badly Heat Damaged Corn (B 2), Sour and Heating Corn (B 39), and Corn Damaged in Various Ways (B 1)

Later the Board of Reviews, Office of Federal Grain Supervision, provided three samples of hand-separated corn kernels representing different forms of damage, for these studies. These samples may be described as follows:

        B1. Kernels representing cob-rot, heat-damage, and other forms of damage common to the lower grades of commercial corn

B2. Badly heat-damaged, or mahogany kernels.

B39. Kernels from a lot of sour and heating corn not, however, badly heat-damaged.

TABLE XIV

RATE OF RESPIRATION OF CORN SAMPLES TAKEN IN A HOT OR HEATING CONDITION FROM CARS
IN THE RAILROAD YARDS AT MINNEAPOLIS

Moisture	Carbon dioxid respired per 24 hours for each 100 grams of dry matter
Per cent	Milligrams
14.8	10.69
15.5	18.91
16.0	24.76
16.6	33.28
17.2	44.89

Portions of each of these samples were brought to different percentages of moisture by the addition of water, and their rate of respiration was determined. These data, as given in Table XV, and graphically in Figure 11, indicate respiratory rates decidedly above that of normal or sound corn. In fact it appears that any cause, such as sprouting or heating, which elevates respiration to a high level, leaves the respiratory "tone" or "pitch" above that of normal corn which has not been so treated. Even tho sprouting or heating grain be cooled and dried, this tendency persists, when comparisons are made with normal corn of the same moisture content and at the same temperature. Damaged corn is accordingly more likely to heat in storage and transportation and its moisture content must be 1.5 to 2 per cent lower than normal corn to insure that it will remain cool as well as the latter. Sour and heating corn was more pronounced in its tendencies toward excessive respiration than the mahogany, or badly heat-damaged, kernels. Possibly disorganization has gone so far in the latter that the "tone" has reached and passed the maximum, and is gradually approaching a lower level.

TABLE XV
RATE OF RESPIRATION OF DAMAGED CORN

Lab. No. B 1. Cob-rotten, heat-damaged, and other forms of damage	
Moisture	Carbon dioxid respired per 24 hours for each 100 grams of dry matter
Per cent	Milligrams
12.48	2.64
14.04	7.32
15.53	17.08
16.55	25.87
17.21	45.08

TABLE XV—*Continued*

Lab. No. B 2.   Badly heat-damaged or mahogany corn kernels

11.08	1.48
12.25	3.57
13.60	7.28
14.62	12.18
15.46	19.59

Lab. No. B 39.   Sour and heating corn

12.39	2.34
13.03	3.78
14.36	8.19
15.14	13.13
17.35	39.31

INFLUENCE OF TEMPERATURE ON RATE OF RESPIRATION

Experience of the trade, as shown by observations of Duvel (1909), Duvel and Duval (1911, 1913), Bailey (1917), and Boerner (1919), has been that when grain begins to heat the rise of temperature per unit of time is greater as the temperature of the bulk becomes higher. Exceptions to this general rule are occasionally encountered when the weather becomes cool, and more heat is accordingly conducted into the atmosphere. Grain in vessels traversing chilled water might also respond to temperature changes of the latter, and the temperature of heating grain in exposed situations changes less rapidly than when not so exposed to cooling effects. Bailey and Gurjar (1918) found that the quantity of carbon dioxid respired by wheat was decidedly increased on raising the temperature by increments from 4° to 55° C. The most rapid change in rate was observed between 35° and 55° C.

In comparing the rate of respiration of shelled corn at two different temperatures, a large sample of composite No. 2 mixed corn, Lab. No. B46, was used. This was divided into six portions, each of which except the first was brought to a different moisture content by adding water. They were then placed in a refrigerator for three days to allow the moisture to penetrate the kernels. At this time the moisture content ranged from 12.08 to 17.70 per cent. Half of each portion was placed in a thermostat at 37.8° C., the other half in a thermostat at 27.8° C. The rate of respiration at 27.8° C. was appreciably lower, being somewhat more than half the rate at a temperature 10° higher. This is shown by the data in Table XVI, and graphically in Figure 12. The ratios at different percentages of moisture are quite uniform, indicating a similar response to increasing moisture content when corn is allowed to respire over a fairly wide range of temperature, providing all comparisons are made at the same temperature.

TABLE XVI

RESPIRATION OF COMPOSITE NO. 2 MIXED CORN AT 27.8 AND AT 37.8° C.

Moisture	Carbon dioxid respired per 24 hours for each 100 grams dry matter		Rate at 37.8° Rate at 27.8°
	At 27.8° C.	At 37.8° C.	
	Milligrams	Milligrams	
12.08	0.68	1.28	1.88
13.89	1.51	2.85	1.89
14.52	2.67	4.98	1.86
16.00	7.21	14.32	1.99
16.51	9.13	17.96	1.97
17.70	23.32	42.21	1.81
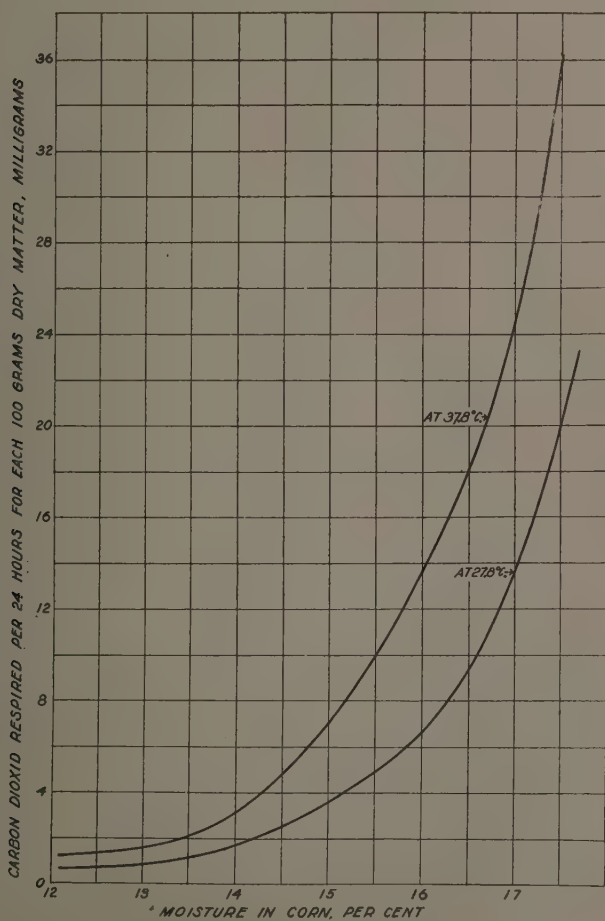
Figure 12. Rates of Respiration of Corn at 27.8° C. and 37.8° C.

CONCLUSIONS

During the curing of husked ear corn the percentage of moisture is appreciably higher in the cob than in the grain during the early stages, but the cob loses moisture at a more rapid rate than the kernels, and as the cob approaches dryness (9 per cent of moisture) the kernels contain more moisture than the cob.

Hygroscopic moisture in shelled corn in equilibrium with atmospheres of different relative humidity at 25° C. varies in different samples of corn. Sweet corn which was used contained a lower percentage of hygroscopic moisture throughout the entire range of humidity studied, and varied from about 7.8 per cent moisture at 35 per cent relative humidity to about 16.5 per cent moisture at 85 per cent relative humidity. White dent corn contained about 8.7 per cent moisture at 35 per cent relative humidity, and about 17.8 per cent moisture at 85 per cent relative humidity, or about one per cent of moisture more than sweet corn throughout the entire range of humidities studied. A sample of white dent corn of the 1919 crop was approximately intermediate between the sweet corn and the dent corn of the 1920 crop.

Distribution of moisture between the germ and the degerminated residue of the corn kernel varied with the moisture content. At higher percentages of moisture the germ contains more moisture than the endosperm, the ratio at maximum imbibition being about 1.5 to 1. At about 18 per cent of moisture both structures contain the same percentage, while as the moisture content of the kernel is further reduced the germ contains less moisture than the residue.

Moisture content in large measure determines the rate of respiration of sound corn stored under uniform temperature and other conditions, as evidenced by the data secured from the study of representative corn varieties grown from Texas to North Dakota. Northern grown corn respired somewhat more vigorously than southern grown corn. Acceleration of respiration with increasing moisture content becomes marked when the moisture exceeds 13 per cent, and increases about 400 per cent between 15 and 17 per cent of moisture. This acceleration is possibly attributable to the altered relation of water to colloidal substances which accompanies the reduction of viscosity of the complex colloidal system in the cellular material. A diminished viscosity within the limits studied in turn apparently accompanies an increased rate of diffusion of dissolved solids and gases in the respiring cells. This is indicated by the potentials and galvanometer deflections produced by the Zeleny electrode when the copper and zinc points of this electrode are inserted into the germs of kernels containing different percentages of moisture. The potentials, or E. M. F., of the small voltaic cells thus produced are almost a linear function of the percentage of moisture

in the kernel, and vary within narrow limits. Deflections of the galvanometer produced by such cells are increased decidedly on increasing the moisture content of the corn kernel, and when plotted against percentage of moisture give a curve of an entirely different character from that resulting from similarly plotting their E. M. F. Thus, raising the moisture content from 14.5 to 17.7 per cent increased the galvanometer deflections by more than 2500 per cent. Since galvanometer deflections are a function of current, it follows that with fairly constant E. M. F.'s in these voltaic cells, their electrolytic resistance varies between wide limits. The resemblance of the curve representing galvanometer deflections, and hence the electrolytic resistance, to rate of respiration when both are plotted against moisture content, suggests that the same physical phenomena are operative in both instances, and that respiration, like electrolytic resistance, is determined by factors influencing the movement of ions and molecules in the cells.

During the curing of corn on the cob immediately after harvest, the rate of respiration is lower for a time than that of corn of the same moisture content later in the season. Possibly a form of dormancy is involved, resulting from a reduced rate of diffusion of oxygen into the respiring cells, or of carbon dioxid therefrom, or both. This condition is of significance in that the probability of heating is diminished during the period immediately after harvest when the moisture content of the grain is usually high.

Cracked and broken corn kernels respire more vigorously than sound, normal kernels, as was shown by comparing the rate of respiration of mixtures containing varying percentages of such material. A somewhat increased risk is accordingly involved in storing and transporting corn containing appreciable quantities of broken grain.

Sprouted kernels when dried until they contain percentages of moisture usual to commercial corn have a higher rate of respiration than sound, ungerminated kernels of the same variety and moisture content. Heat damaged, and sour and heating corn also respire more vigorously than sound corn containing the same percentage of moisture. It appears that conditions such as heating or germination which for a time accelerate respiration, leave the grain with a higher respiratory "tone," even after the accelerating influence is removed by cooling and drying. Such grain accordingly presents a greater hazard in commercial handling and storage than sound grain of the same moisture content.

Temperature affects the rate of respiration, an increase of ten degrees, from 27.8° to 37.8° C. nearly doubling the rate throughout the range of moisture studied. This is about the increase found in enzymic and other chemical reactions for each 10° C. increase, within the limits of temperature involved in this instance.

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APPENDIX

TABLE XVII

RATE OF RESPIRATION OF MINNESOTA No. 13 CORN, FROM UNIVERSITY FARM, ST. PAUL MINN., LAB. No. 6854

Moisture Per cent	Carbon dioxid respired per 24 hours for each 100 grams of dry matter Milligrams
10.48	0.64
11.63	1.10
12.52	1.63
13.37	3.04
14.19	4.38
15.17	8.40
16.26	18.20
17.09	39.67
18.01	80.30

TABLE XVIII

RATE OF RESPIRATION OF WHITE FLINT CORN, FROM FARGO, No. DAK., LAB. No. 6855

Moisture Per cent	Carbon dioxid respired per 24 hours for each 100 grams of dry matter Milligrams
10.42	0.73
11.11	0.85
12.87	1.25
13.88	2.01
14.53	3.68
15.35	7.51
15.96	12.25
16.42	19.33
17.03	39.10
18.09	82.70

TABLE XIX

RATE OF RESPIRATION OF TUXPAN CORN, FROM DALLAS, TEXAS, LAB. No. 6858

Moisture Per cent	Carbon dioxid respired per 24 hours for each 100 grams of dry matter Milligrams
11.53	0.82
12.62	1.34
13.49	2.17
14.38	3.46
15.28	7.56
16.19	14.52
16.85	24.25
17.22	29.67
17.94	55.12

TABLE XX

RATE OF RESPIRATION OF REID'S YELLOW DENT CORN, FROM AMES, IOWA, LAB. NO. 6859

Moisture Per cent	Carbon dioxid respired per 24 hours for each 100 grams of dry matter Milligrams
10.24	0.55
11.62	1.03
12.97	2.14
14.04	3.51
15.26	5.37
16.30	10.52
16.64	13.75
17.16	18.86
17.46	23.94
18.05	44.67

TABLE XXI

RATE OF RESPIRATION OF COMMERCIAL WHITE CORN, FROM COLUMBIA, MO., LAB. NO. 6860

Moisture Per cent	Carbon dioxid respired per 24 hours for each 100 grams of dry matter Milligrams
10.67	0.77
11.56	1.18
12.45	1.96
13.51	3.20
14.56	5.00
15.37	7.58
16.16	12.01
17.36	31.08
18.11	55.20

TABLE XXII

RATE OF RESPIRATION OF MEXICAN JUNE CORN, FROM PHOENIX, ARIZ., LAB. NO. 6861

Moisture Per cent	Carbon dioxid respired per 24 hours for each 100 grams of dry matter Milligrams
10.73	0.58
11.47	0.82
12.33	0.90
13.45	1.93
14.52	4.25
15.40	9.01
15.93	11.98
16.52	16.41
17.36	28.87
18.14	34.78

TABLE XXIII

RATE OF RESPIRATION OF REID'S YELLOW DENT CORN, FROM COLUMBIA, MO. LAB. NO. 6862

Moisture Per cent	Carbon dioxid respired per 24 hours for each 100 grams of dry matter Milligrams
11.68	1.37
13.41	2.20
14.64	3.53
15.57	7.60
16.06	10.24
17.19	20.54
18.17	49.92

The University of Minnesota
Agricultural Experiment Station

Wages of Farm Labor

By C. L. Holmes
Division of Agricultural Economics

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Wages of Farm Labor

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Division of Agricultural Economics

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By C. L. HOLMES

INTRODUCTION

The purpose of this bulletin is to analyze the wages of hired farm labor in Minnesota. This involves making comparisons by sections of the state and by systems of farming, and also tracing the changes in wage levels leading up to the present. Accounting for the sectional differences in wages has required some analysis of the various systems of farming in the state; and accounting for the shifts in wages has required an analysis of changes in the proportions of land, labor, and equipment, and the returns to these. This analysis is especially interesting during the last few years.

The collecting of the data for this study made necessary a comparison of three different methods of collecting wage data, (1) the method of reporters' estimates, used by the United States Bureau of Crop Estimates; (2) the census method, represented by the state census of 1920, made by the Minnesota State Department of Agriculture; and (3) the sample data method, represented by a special inquiry conducted by the Division of Agricultural Economics, assisted by the United States Bureau of Crop Estimates. For studying the first method, the Minnesota field agent of the Bureau of Crop Estimates furnished the actual schedules of the inquiry of December, 1919. The returns from the census method are available in the 1920 state census reports. The special inquiry used with the third method was sent to 7500 farmers who employed labor in 1919. More than 1500 of these replied, giving information concerning more than 2500 hired men. The returns were scattered fairly uniformly over the state.

CLASSIFICATION OF FARM LABOR

The importance in Minnesota farming of family and hired labor relative to the farmer's own labor is shown by the federal census. Table I shows the total number of farmers and farm laborers 16 years of age and older from 1880 to 1910. (See also Fig. I.) Altho the farmer himself still supplies the major portion of labor on Minnesota farms, the proportion supplied by his helpers has steadily increased as farming has shifted from pioneer conditions and the amount of farming business conducted by one man, and on a given area of land, has increased. Between 1880 and 1910 there was a shift of 14.2 per cent in the proportion between the number of farmers and the number of their mature

helpers.[1] This change is due partly to the gradual shift from almost exclusive grain farming to systems in which livestock enterprises, particularly dairying, form an important part, but more largely to the gradual adjustment in all types of agriculture to the most profitable size of business as measured not only in area of land used but in men employed and total funds invested. Compared with many other enterprises, the most profitable business unit in farming is not large as measured by the labor used, but it is undoubtedly larger than the one-man farm. Hence, as farming develops from the pioneer stage, there is normally a change not only in the direction of more careful and intensive use of the land, but toward a somewhat larger amount of labor under each manager. Along with these changes goes necessarily a considerable increase in the total investment necessary to carry on a farm business.

TABLE I

NUMBER AND CLASSIFICATION OF MALES 16 YEARS OF AGE AND OLDER ENGAGED IN AGRICULTURE
IN MINNESOTA, 1880–1910

Date	Number			Percentage		
	Total	Farmers	Laborers	Total	Farmers	Laborers
1880	122,683	93,386	30,297	100	75.4	24.6
1890	168,552	116,851	51,701	100	69.3	30.7
1900	234,658	154,659	79,979	100	65.9	34.1
1910	255,022	156,137	{ 47,837* { 51,048†	100	61.2	{ 18.8* { 20.0†

* Hired men.
† Farmers' sons.

It is only with the census of 1910 that we get any measure of the relative importance of hired labor and that of the farmers' sons. In that year, agricultural laborers were reported as "on the home farm" or "working out." For Minnesota, these two groups were very nearly equal. (See Table I and Fig. 1.) There were about one hired man and one son 16 years of age or older at work on the home farm for every three farms in the state. If this additional labor had been distributed as evenly as possible among all the farms, 57,252 or approximately one third of the farms, would have been operated by the owners alone, while the remaining 98,885 farms would each have had one additional laborer.

It is to be kept in mind, however, that these census figures were collected in the spring and therefore could have included only a small part of the great body of transient laborers who enter the farming sections

[1] Women, and children under 16, are omitted from these figures, but it is not likely that the proportion of such labor has changed greatly.

of the state for harvest, threshing, and other fall work, and who, in view of our prevailing type of agriculture, constitute almost as important an element in the farm labor supply as do the hired men who work by the season or year.
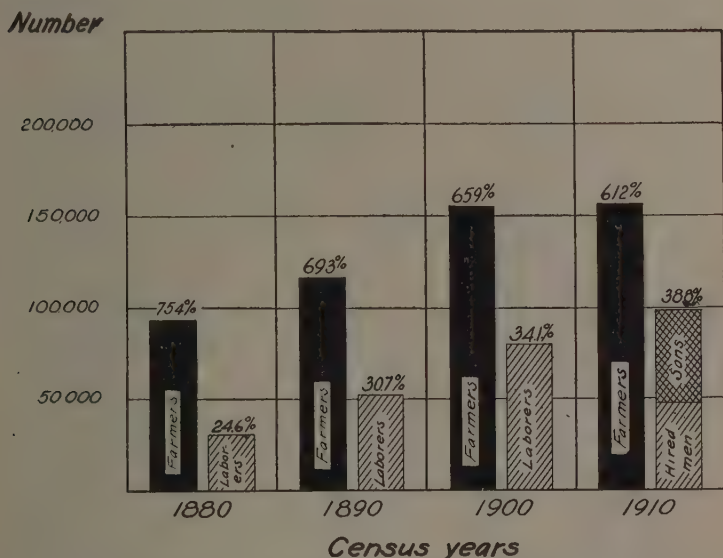
Fig. 1. Number and Classification of Males 16 Years Old or Older Engaged in Agriculture in Minnesota, 1880-1910

Farm laborers were increasing more rapidly than farmers during each decade. However, most of the farm work is still done by the farmers themselves.

RELATION OF TYPES OF FARMING TO WAGES

Before attempting to analyze wages for the season of 1919, particularly the sectional variations in wages, we must know something about farming conditions in the various parts of the state. There are in the North Central states at least three well-defined systems of agriculture. These are (1) corn-and-livestock or Corn Belt farming, centering in Iowa and Illinois; (2) small-grain farming, centering in North Dakota; and (3) dairying, centering in southern Wisconsin.

Located between the centers of these types of agriculture, Minnesota is the meeting ground of all of them. A large part of the state is the transition zone between the well-defined type areas of neighboring states. Hence, except in the northwestern part, types of farming do not stand out distinctly. There are enough differences, however, to affect greatly the labor problem, and it is therefore important to point them out as far as possible and to outline as accurately as may be the geographical limits of the several types of farming. These limits were originally

drawn on the basis of the 1910 U. S. Census reports but they have been
checked against the 1920 census data and all changes since 1910 are
carefully pointed out in the page following. Figure 2 shows the rela-
tive acreage of the various crops in each of the counties of the state.
The size of the circles represents the average area per farm of all crops,
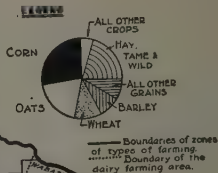
Fig. 2. Crop Acres per Farm and Percentage in Various Crops, by Counties, 1909
     The heavy lines are the boundaries of the type-of-farming sections numbered I to VII
described in the text. The dotted line indicates the limits of the area in which dairying was
most important according to the 1920 U. S. Census.

including tame and wild hay but excluding pasture. The sectors within the circles show the average percentage of this total area occupied by the different specified crops. Such a map reveals the geographical variations in the type of farming as far as they can be revealed by cropping systems, but it shows nothing as to livestock enterprises except as inference may be drawn from the crops grown. To supplement this map,
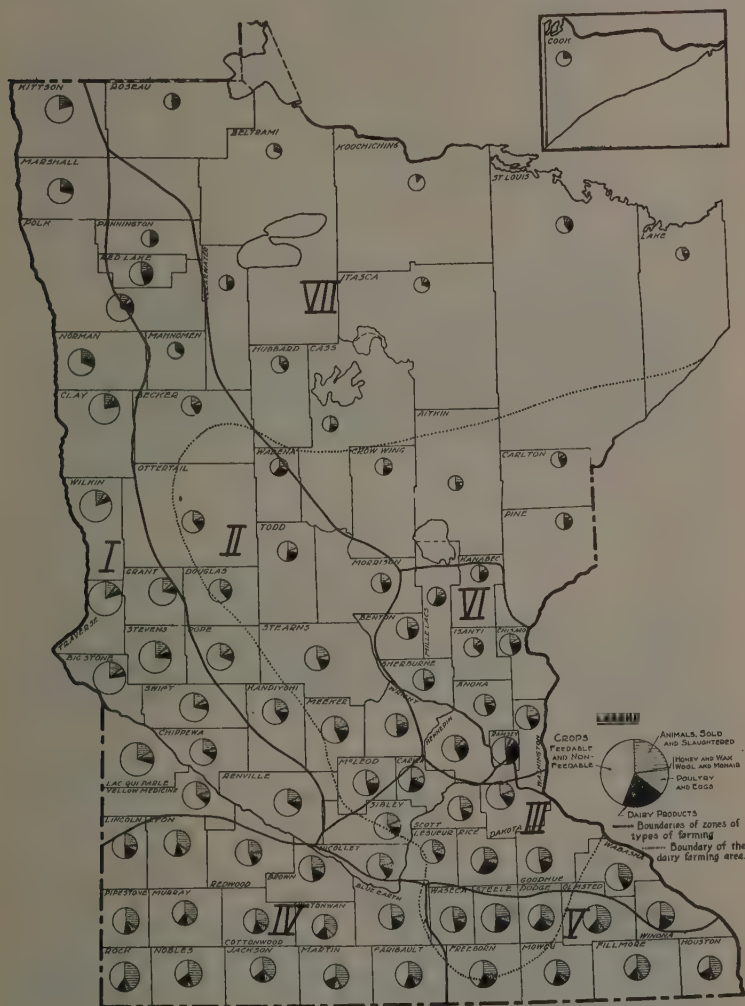
Fig. 3. Gross Income per Farm and Percentage Derived from Various Sources, by Counties, 1909

Type-of-farming areas are outlined as in Figure 2. Note the varying importance of small grains, dairy products, and livestock as sources of income in the several parts of the state. The largest average gross income per farm was in Traverse County and was $2353.

Figure 3 was constructed, showing by counties the relative average size of the farmer's gross income for 1910 and the average percentage of it coming from different specified sources in each county. Not enough of the 1920 census data are available for a new analysis of sources of income, but those that are available indicate that the map is sufficiently accurate for the purpose in mind. This classification of the sources of income is not as detailed as might be desired. For example, the census does not separate the receipts from different classes of livestock. As it stands, however, the gross receipts map shows very strikingly the regions where cash crop production overshadows other enterprises, where dairying is important, and where the sale of meat animals figures largely as a means of disposing of crop products.

On the basis of these two maps and such supplementary information as was available, the state has been rather tentatively divided into the seven more or less distinct type areas outlined on the maps presented in the bulletin. Following are brief descriptions of the type of agriculture and its effect on the farm labor problem in each of these sections.[2]

SECTION I. NORTHWEST SMALL GRAIN SECTION

This section, which includes the Minnesota portion of the Red River Valley and the upper part of the Minnesota River Valley, is the most clearly defined farm type area in the state. There is a high degree of uniformity in selection of crops, methods of crop disposal, seasonal demands for labor, and the organization of the farm business generally.

Owing to the great importance of small grain, the type of farm organization in these counties is one in which a large amount of land and a comparatively small amount of labor is used.

Moreover, the seasonal distribution of labor is very uneven. (See Fig. 4.) There is a rush season in the spring, occasioned by seeding a big acreage, in which all the labor is practically that of handling teams and machinery. This is followed by a slack period while the grain is growing and ripening. Then comes the harvest and threshing season in which there is a great deal of hand labor, as well as team and machine

[2] This division of the state does not designate any portion as a distinct dairy section. The 1910 United States census revealed no counties where dairy products were the leading source of farm income and where the farm organization centered unquestionably in the dairy enterprise. However, between 1909 and 1919, dairying increased in importance in Minnesota. One set of figures shows that there were 71 dairy cows for every 1000 acres of improved land in Minnesota in 1919 as compared with only 55 in 1909. That these figures are not exactly comparable is evidenced by another set of figures which show 22.1 gallons of milk per improved acre in 1919 compared with 20.4 gallons in 1909. The census bureau used a new definition for dairy cow in 1919. In Figures 2 and 3 a dotted line has been drawn to include that part of the state which may be called the dairy section. Within this area in 1919 at least 90 dairy cows were kept for every 1000 acres of improved land, or the receipts from dairy products were at least $4 per improved acre, or the milk production was at least 22 gallons per improved acre. In drawing this line due allowance was made for the pasturage obtained from unimproved land in the northern counties.

work, in which the regular labor force must be supplemented by day
laborers, hired at high wages and for a comparatively brief period.
While many farmers operate farms so large that they need hired help
through the entire season, practically all of them are dependent on
casual labor during the late summer and early fall. This labor is re-
cruited from the so-called casual labor class who drift from place to
place and from job to job. Frequently they are industrial laborers a
part of the year. Depression in industry may create an oversupply; and
prosperity in industry a scarcity.
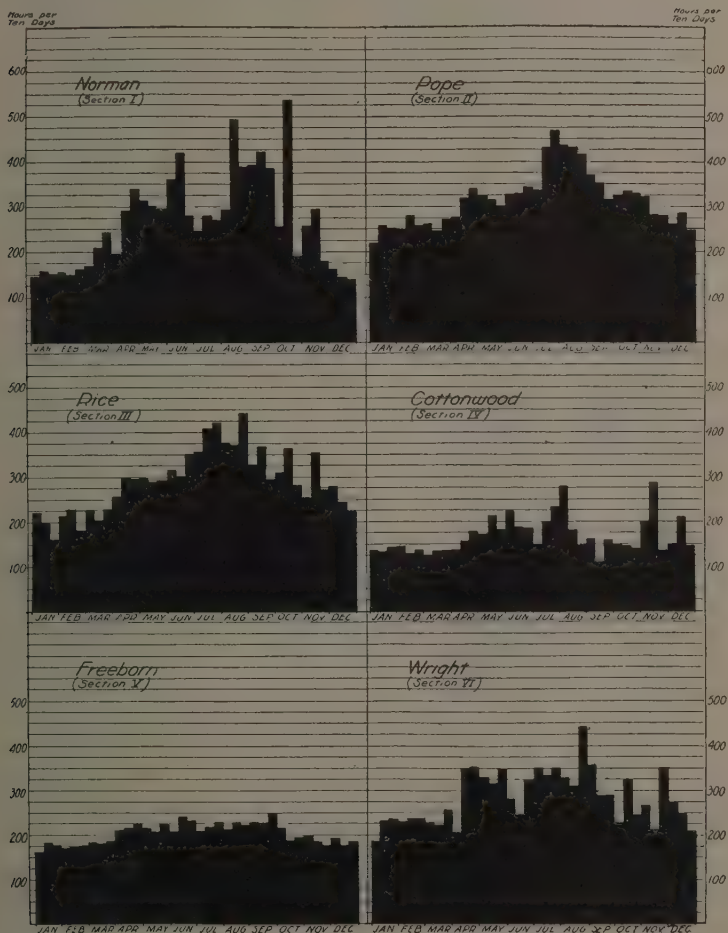
Fig. 4. Seasonal Distribution of Labor by Ten-Day Periods on Specific Farms Located in
Six of the Type-of-Farming Sections

Farmers in regions where the seasonal distribution of labor is very uneven normally pay
more for their hired labor because wages tend to be highest when the demand for labor is
greatest. (See Table VIII.)

SECTION II. CENTRAL SMALL GRAIN SECTION

This section differs in its farming from Section I principally because of a higher proportion of untillable land which has to be utilized for pasture and hay. This gives livestock a larger place in the farming. Since the farms are smaller, the farmers and their families more nearly supply the needed labor. Likewise the substitution of livestock for small grain makes the seasonal distribution of labor demand somewhat more even and reduces the demand for extra help in harvest. The labor problem is for these reasons appreciably less acute here than in the more highly specialized small grain area.

SECTION III. SOUTHEASTERN SMALL GRAIN SECTION

The line separating this section from Section II, as shown in Figures 2 and 3, is rather arbitrarily drawn, tho conditions within the two sections are distinctly different except on the margin. The land is of better quality in this section and its nearness to St. Paul and Minneapolis affects the agriculture considerably. Tho small grain is the most important product, livestock, particularly dairy cattle, holds a large and growing place in the farming system.

Because of the greater importance of corn and livestock, and particularly because of the dairy work, the need for labor is continuous throughout the year and subject to less seasonal variation than in the other small-grain regions. Further, because the farms are larger and have more livestock, they require much more farm labor. More of it, however, is hired by the year than in the other two sections.

This type of farming, moreover, requires a better class of laborers than is needed in simple grain farming. Dairying and other livestock work require more skill, better judgment, and greater trustworthiness than the handling of teams and implements. Fortunately this type of farming tends to keep in local employment a larger proportion than usual of the young men trained in the local farm practice and hence well suited to the local farm work.

SECTIONS IV AND V. CORN AND SMALL GRAIN SECTIONS

The agriculture of the southern portion of Minnesota has been greatly affected by the gradual increase in the corn acreage. The north-- ern boundary of these two sections as given on the maps was determined for the most part by the 20 per cent corn line. That is, almost all the counties in which corn, according to the 1910 census, occupied 20 per cent or more of all the land in crops, including hay, were placed in these two sections. By 1919, however, this line had shifted northward considerably—Yellow Medicine, Renville, Chippewa, Nicollet, and Le Sueur counties had more than 20 per cent of crop land in corn.

In 1909, corn occupied 24 per cent of the crop area in Section IV and only 19 per cent in Section V; and in 1919 the percentages were 27 and 18 for the two areas. On the whole, livestock is considerably more important as compared with crops in Section V than in Section IV.

The farm labor problem is also different in these two sections. There is a larger demand for hired labor in Section IV because the farms are larger, the typical farm being from 225 to 300 acres with from 200 to 275 acres improved; while in Section V the typical farm is not over 160 acres with from 90 to 100 acres improved. In Section IV, therefore, much labor must be hired. The dairying in Section V requires much more labor in proportion to the area occupied, particularly for the work which lasts throughout the season or year, than does the raising of cash grain and meat animals, but it is of a kind that can be done to a large extent by the farmer and his family. In Section IV, the seasonal demand for labor is not greatly different from that of Section I, for the acreage of small grain per farm is large, notwithstanding the importance of corn and livestock. The seasonal labor demand of Section V resembles that of Section III. (See Fig. 4.)

SECTION VI. POTATO, TRUCK, AND HAY SECTION

Physical and economic conditions combine to make the agriculture of Section VI distinct from that of all other parts of the state. Altho dairying is a profitable enterprise and considerable income is secured from the sale of cattle and some swine, crops are the most important source of income.

The labor problem in this region is somewhat unusual. The seasonal demand for labor is very irregular. There is a little call for extra labor in grain harvest, but the heaviest demand comes with the potato harvest in September. The truck farmers need large amounts of labor at various times during the season for hand work in planting, weeding, hoeing, and harvesting their products. For much of this labor they depend on boys and men from the cities. The farms are small, and hence few year-round men are needed.

SECTION VII. THE UNDEVELOPED SECTION

The northeastern two-fifths of the state has been arbitrarily included in a single type of agriculture. For the purpose of this bulletin, this is sufficiently accurate. Some differences are already to be noted in the sort of farming practiced in the different settlements, but these do not affect the labor problems greatly.

Hired farm labor is not a matter of much importance in this region. There are a few large farms where help is kept, but for the most part

TABLE II

RELATIVE IMPORTANCE OF THE SEVERAL TYPES OF FARM LABOR CONTRACTS IN MINNESOTA, 1919

Types of contracts	Number of contracts								Percentage of total number							
		Sections								Sections						
	State	I	II	III	IV	V	VI	VII	State	I	II	III	IV	V	VI	VII
By the month for the year....	318	72	51	48	64	39	26	18	12.8	9.2	13.5	17.5	15.1	14.4	14.9	8.9
By the month for the season...	563	166	72	61	138	66	29	31	22.4	21.2	19.1	22.3	32.5	24.4	16.6	15.3
By the month for first half of the season..............	120	38	27	17	19	9	6	4	4.8	4.9	7.1	6.2	4.5	3.3	3.4	2.0
By the month for second half of season	153	43	28	20	30	18	6	8	6.1	5.5	7.4	7.3	7.1	6.6	3.4	3.9
By the month for the winter....	146	40	28	16	24	26	6	6	5.8	5.1	7.4	5.8	5.6	9.6	3.4	3.0
By the day for harvesting, threshing, silo filling, etc....	728	310	103	65	104	63	30	53	29.0	39.6	27.2	23.7	24.4	23.2	17.2	26.1
By the day for other work....	480	113	69	47	46	50	72	83	19.1	14.5	18.3	17.2	10.8	18.5	41.1	40.8
Total	2508	782	378	274	425	271	175	203	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

the settler and his family do all the work except for short periods when special work may require outside help. This results in most of the hiring being by the day rather than by the month.

The small volume of the farm business on the typical settler's farm makes the farmer himself a hired man for a considerable portion of the year. He works in the lumber camps, the sawmills, and even in the North Dakota wheat fields, in order to supplement the farm income in the years when he is "making" his farm.

FARM WAGE CONTRACTS IN 1919

Two of our sources of information furnish data on the relative number of hirings for different lengths of time or for different parts of the year. The Minnesota state census blank contained two inquiries on farm labor. The first asked the monthly wage rate paid in summer and the second the monthly wage rate paid in winter for the year 1919. The comparative number of farmers answering the first and the second of these questions may be taken as a measure of the relative demand for hired help during the crop growing season and the winter months. (See Table VI.) In the special schedule of inquiry on farm labor sent to farmers, the correspondents were asked to report the actual dates between which the men were employed and the time unit, as month or day, on which wages were based. The results of this are given in Table II.

In general, the greater the permanence of the work and the more evenly distributed the labor demands, the longer the term of the contract. Farmers seek to save expense by hiring only for the part of the year when help is needed, provided the slack time is not so short as to make the saving not worth while. Hiring by the year indicates a type of farming in which livestock enterprises are so important that hired labor is needed during the winter months when no field work can be done. Such hiring is most frequent in well-developed dairy sections. A more common type of labor bargain is one which covers only the crop season beginning about the first of March and extending to the first or the middle of November. This kind of hiring along with day hiring prevails in sections where the farming is based primarily upon crop enterprises. Still another kind of contract is that covering labor for the winter months. This, presumably, is supplementary to the season contract, the two together being equivalent to the year-round term. This arrangement may be more satisfactory in some cases because it gives a better opportunity to adjust the wage to the relative value of the hired man's time at the different seasons of the year and to differences in the supply of labor. Hours of labor are commonly somewhat shorter and the supply of laborers is greater in the winter, and the wages paid on these winter contracts are almost invariably

lower than for the crop season or year. Such an arrangement is desir-
able if there is danger that the hired man will break his year contract
in the spring, or that the employer may arbitrarily dismiss his man with
the close of the crop season.

A still further adjustment in this direction is to be found in the
spring and fall contracts, numerous cases of which were found in this
investigation. Under this arrangement, help for the first half of the
crop season—say from March 1 to July 1—would be contracted for at
one wage level. This would be supplemented with another contract,
often with the same man, at a considerably higher figure for the re-
mainder of the season. The greater demand for labor in the latter half
of the season, with a resulting higher scale of wages, makes this adjust-
ment desirable if the laborers can not be depended upon to keep their
contracts. A few cases were found in which a different wage rate was
arranged for practically every month of the season.

In all the foregoing types of contracts, the unit of time on which
payment is based is the month. This time unit is the basis for prac-
tically all the more permanent classes of wage agreements where the
work is such that the farmer needs continuous help over a considerable
period. Under this arrangement, no payment is ordinarily deducted for
loss of working time due to unseasonable weather, breakdown of ma-
chinery, and the like. The rate is somewhat lower than where these
deductions are made, even tho the efficient farm manager may be counted
upon to have a variety of tasks planned to take the time of his men in
such emergencies. For special work of short duration, such as harvest-
ing, threshing, silo filling, and construction work, the time unit is almost
always the day. Wages are at a somewhat higher rate and time is regu-
larly counted only when the special tasks are under way. Frequently the
farmer boards these special laborers during interruptions from rain or
other causes in return for part time incidental work.

Tables II and V contain the available evidence as to the relative
importance of these various types of wage contracts in the state. Table
VI (see page 20), made up of figures from the state census, has the
advantage of being based on a complete canvass of all the farmers in
the state, and the disadvantage of showing only two types of contract,
summer and winter. Table II contains figures on a much larger number
of types of contracts, but is based on the returns of only about 1500
farmers.[3] The discussion following is based on these 1500 returns.

This inquiry shows that for the state as a whole, month and day
labor are of almost equal importance so far as the relative number of

[3] This is approximately one per cent of the whole number of farmers in the state. By
this method one is able to get very much more detailed information than can ordinarily be
obtained from a broader inquiry like a census. The danger is that his returns may not make
a fair sample. However, it is believed that the number of farmers returning information in
this inquiry is sufficient to be fairly representative.

hirings are concerned. Of the 2508 hired men reported, 1300, or ap-
proximately 52 per cent, were engaged by the month, and 1208, or 48
per cent, were paid by the day. Of course, in amount of work done,
the month men are much more important. Of the month men, those
hired for the season are most numerous, followed by those hired by
the year. Relatively few are hired for the winter months only, or
for the first or second half of the crop season. Of the day men, those
hired for work in harvesting and caring for crops are 50 per cent more
numerous than those engaged for other work. Those hired by the
day for "other work" were for the most part engaged in the spring
months, and the work was very largely clearing and preparing land.
The cases of all special artisans, such as carpenters and masons, were
excluded from the figures in order to restrict the study to ordinary
farm work.

When these figures are examined for the various types-of-farming
sections, many significant variations are found. For example, the
number of day contracts reported is greater than the number of month
ocntracts in Sections I, VI, and VII, but fewer than the number of month
contracts in the other four sections. This is accounted for in Section I
by the large amount of extra harvesting and threshing labor needed
to care for the small grain crops. Three times as many day hands
were hired for this sort of work as for other day work. In Sections
VI and VII the excess of day laborers over month laborers is due not
so much to harvest work as to other special work of short duration.
In Section VI this special work is largely on truck crops, while in
Section VII most of the farms are operated on such a small scale that
it does not pay to keep hired help continuously, so that day labor tends
to be the prevailing type for the whole area. This is clear from the
figures in Table II. In Sections II, III, IV, and V, the excess of
month contracts over day contracts is due (1) to livestock farming and
types of cropping which go with livestock farming, all of which make
for more continuous and less irregular demands for labor, and (2) to the
larger farms and farm business, which require a larger proportion of
hired help.

As for the month contracts, almost twice as many are for the season
as for the year. Hiring by the year is more frequent in Sections II,
III, V, and VI, where dairying is most important, than in Sections I
and IV.

Another method of hiring farm work done, not indicated in Table
II but nevertheless of some importance in the state, is that of paying
on a piece-work basis. Corn husking, corn shelling, and the threshing
of small grains are paid for by the bushel. Certain field operations,

such as cutting grain and plowing with a tractor, are paid for by the acre. This type of hiring, like hiring by the day, is resorted to in the case of special tasks of short duration. Data were not collected on piece-work rates.

FARM WAGES IN 1919

The farm labor situation existing in 1919 was in many respects abnormal. The war had greatly increased the production of some farm products to the curtailment of others, and this abnormal crop situation still existed in 1919, as evidenced particularly in the high acreage of wheat. It was during this season that prices on general commodities were advancing most rapidly and producers in nearly all non-agricultural lines were bidding strongly for labor. The normal supply of farm labor was greatly depleted by the war, and altho by the spring of 1919 demobilization was nearly completed, many thousands of former farm hands had not yet settled down in their old surroundings. The supply of farm labor was therefore very short. It was still short in the spring of 1920. Wages for the approaching crop season promised to be higher than most farmers could afford to pay. There was widespread apprehension of a serious reduction of crop acreage. Some creditable authorities went so far as to predict an acute food shortage.

THE WAGE LEVEL

One of the things attempted in this bulletin is to determine what may be called the level of wages for farm labor in different sections of the state and at different seasons. This introduces the idea of a "wage level," which probably needs to be explained. The level of wages for labor, like the level of prices for wheat, grows out of supply and demand. The only real demand for farm labor comes from those farmers who stand ready to pay a given known wage; and the only real supply is made up of the labor of men who, in view of all their other opportunities for employment, stand ready to accept farm work at a given wage. The wage level of any given season is the result of a balancing of what employers will pay and what the men will take. Both the wages offered by the farmers and the wages asked by the men affect this balancing point. There are marked differences between farmers as to how high a wage they can safely pay. These differences are due mainly to the relative business ability of the farmers and to differences in the type of farming. Similarly, there are differences in the minimum wage of the various farm laborers because not all laborers have equal opportunity and equal ability to take up other lines of occupation. This whole situation may be illustrated by means of assumed figures of wages and labor demand and supply at various

wage levels. Suppose that in a certain county the number of jobs actually open and the number of men actually willing to work at various wage levels from $20 to $90 per month, are as follows:

Wages per month	Number of jobs open	Number of laborers ready to work
$20	175	10
30	125	40
40	110	75
50	100	100
60	90	110
70	80	120
80	60	130
90	40	145

Under these assumed circumstances, if wages were $20 per month, 175 men would be wanted with 10 available, while at $90 only 40 jobs would be open and 145 men willing to work; but at $50 per month just as many men are ready to work as there are jobs to fill, and wages in that county for the particular kind of work in question are established at about $50 per month.

The wage level for a state, however, or even for a neighborhood, is not so definitely determined as the foregoing would indicate. There are many different kinds of work for which men are hired and many different grades of men seeking work, and these differences make for variations in wages. Further, the farmers seeking to hire men and the men looking for jobs do not all get together at one bargaining place as do the buyers and sellers of produce in a market. Hence, competition in the labor market has less chance to reduce all wage bargains to a common level than is true in the buying and selling of goods.[4] In Table IX (page 32), showing day wages by weeks for the entire season of 1919, there is a wide difference between the lowest and the highest wages paid. Table III shows a similar situation with reference to the wages of men hired by the month for the season. In this table the data are divided according to type-of-farming sections, but even within these narrower geographical limits, the range of wages is wide. Even within a township, there would be a considerable range.

On the other hand, these tables show an unmistakable tendency toward the establishment of a definite wage level. Very few men are hired at the extremely low figures and comparatively few at the highest figures. The point between these extremes at which most of the hiring is done, may fairly be taken as the level toward which wages are tending.

[4] The fact that a wage contract is normally for a period of time—a month, a season, or a year—tends also to prevent a perfect adjustment of all wages for a given kind of labor to a common level. The longer the term the further a wage determined by past forces is projected into the future and the further above or below subsequently determined wage levels it will be.

In other words, it is the real wage level. During many weeks, there are two or more wage points at which much hiring is done. There seems, therefore, to be more than one level. This may be accounted for in the case of day labor in several ways. It may represent the difference in wages for different kinds of work at the same time, different wages for the same work in different parts of the state, or a difference in the quality of the men with respect to the work they are doing.

TABLE III

NUMBER OF MEN REPORTED HIRED BY THE MONTH FOR THE SEASON AT THE SEVERAL WAGE LEVELS, MINNESOTA, 1919

(Sample data)

Wage group	State	Type-of-farming section						
		I	II	III	IV	V	VI	VII
$22.50–$27.49	1	..	..	..	..	..	1	..
27.50– 32.49	1	..	..	..	..	..	..	1
32.50– 37.49	5	..	..	1	1	2	..	1
37.50– 42.49	20	6	..	6	2	1	2	3
42.50– 47.49	24	3	6	2	3	5	5	..
47.50– 52.49	141	37	19	14	34	17	7	13
52.50– 57.49	51	24	7	8	4	6	..	2
57.50– 62.49	123	33	15	16	35	15	4	5
62.50– 67.49	71	22	10	8	13	8	8	2
67.50– 72.49	24	3	7	..	6	5	2	1
72.50– 77.49	35	12	3	2	15	1	1	1
77.50– 82.49	14	3	1	1	7	..	2	..
82.50– 87.49	9	1	1	2	5	..	..	..
Wage per month	58	59	58	57	61	56	55	54

These two tables also reveal in a striking way the shifts in the wage level. Table IX shows such shifts with the seasons. Evidently the level rises decidedly as the season advances until the peak of the harvest season is reached, and then declines. Table III shows that wages may be at one level in one part of the state and at an entirely different level in the same season in other parts.

The figures cited would seem to show that, notwithstanding the various opposing circumstances, there is a tendency toward a common wage level and that this level moves up or down in response to the influences already mentioned.

WAGE DATA FOR 1919

Reference has already been made to the sources of information on farm wages for the season of 1919. Table IV gives the results of the 1500 returns received from employing farmers. It presents, by sections and for the state as a whole, the wages for all the types of contracts already described as well as the averages of the farmers' estimates of the value of the board and other non-money payments included in the hired man's total wage.

TABLE IV

Average Rates of Farm Wages in Minnesota for 1919
(Sample data)

Type of contract	State	Type-of-farming sections						
		I	II	III	IV	V	VI	VII
By the month hired for the year	$55.00	$57.00	$54.00	$53.00	$55.00	$55.00	$56.00	$56.00
By the month hired for the season	58.00	59.00	58.00	57.00	61.00	56.00	55.00	54.00
By the month hired for first half of season	53.00	54.00	52.00	43.00	60.00	54.00	48.00	57.00
By the month hired for second half of season	71.00	72.00	75.00	69.00	71.00	64.00	65.00	72.00
By the month hired for the winter	36.00	28.00	38.00	34.00	46.00	38.00	38.00	42.00
By the day hired for harvest, silo filing, etc.	4.75	5.00	4.25	4.75	5.00	4.25	4.00	4.00
By the day for other work	3.00	3.00	3.00	3.00	3.50	3.00	3.25	3.00
Value of board, etc., per month, month contract ...	24.00	26.00	25.00	23.00	27.00	25.00	21.00	24.00
Value of board, etc., per day, day contract	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

TABLE V

Estimated Wages of Farm Laborers in Minnesota for 1919
(Bureau of Crop Estimates, U. S. Department of Agriculture)

Type of contract	State	Type-of-farming sections						
		I	II	III	IV	V	VI	VII
By the month, hired by the year with board	$54.00	$57.00	$51.00	$52.00	$55.00	$58.00	$52.00	$52.00
By the month, hired by the year without board	75.00	77.00	74.00	75.00	75.00	80.00	76.00	70.00
By the day hired for harvest with board	4.50	5.00	4.00	4.75	4.75	4.50	3.75	3.30
By the day hired for harvest without board	5.00	6.00	4.75	5.50	5.75	5.25	4.50	4.00
By the day hired for other work with board	3.50	3.75	3.25	3.50	4.00	3.75	3.00	3.00
By the day hired for other work without board	4.25	4.75	4.00	4.25	4.75	4.00	4.00	4.00

TABLE VI

Average Rates of Farm Wages in Minnesota for 1919 as Reported by the State Census of 1920

Type of contract	State	Type-of-farming sections						
		I	II	III	IV	V	VI	VII
Hired for the summer, number of farmers reporting	40,753	10,074	8,028	6,268	7,192	3,876	3,449	1,866
Hired for the summer, wages per month	$60.00	$58.00	$61.00	$59.00	$63.00	$58.00	$61.00	$64.00
Hired for the winter, number of farmers reporting	11,815	2,352	2,464	2,417	1,320	1,325	1,228	708
Hired for the winter, wages per month	$42.00	$40.00	$40.00	$39.00	$43.00	$39.00	$45.00	$57.00

Table IV gives the results of the estimates of the prevailing rates of wages in 1919 made by 350 farmer correspondents of the Bureau of Crop Estimates of the United States Department of Agriculture. These are represented in the form of averages for the same geographical divisions as are followed in the former table. The wage is reported in terms of the amount of cash paid both with and without board. Only a few types of contracts are included.

Figures derived from the report of the state census are given in Table VI. In this report we have but two types of contracts, those for men hired for the summer and those for men hired for the winter, both on the month basis of pay. Presumably the summer wage as given in reply to the census inquiry covers practically the same portion of the year as the season rate given in the replies to the special inquiry. The winter contracts reported in both should cover practically the same months of the year; however, it appears that many month wage rates on year contracts were included in the state census figures. In this census, nearly 41,000 farmers hiring for the summer and nearly 12,000 hiring for the winter reported their wage rates. This, presumably, includes all farmers who hired labor by the month that year, except a comparatively small number whose replies indicated that they had misunderstood the questions.

The rates given in these tables do not include the farm laborer's board and lodging and other extras. It is so commonly understood that a farm hand is to receive board and lodging in addition to his money wage that it is frequently not mentioned in the bargaining. Other compensations in the nature of personal service, such as washing and mending, are not so uniformly included, and if received are usually specified in the agreement. The returns from farmers on this point mentioned a variety of items not uniformly received. A frequent one was the keeping of the hired man's driving horse or the use by the hired man of the farmer's driving horse and buggy, and in at least two cases the use of an automobile was specified as a part of the hired man's compensation. The significance of these non-cash elements in the wage of the farm laborer is too frequently lost sight of in wage discussion. The farmer himself frequently underestimates their actual value, and the hired man and others, in comparing farm wages with those in other industries, fail to give them due weight.

COMPARISON OF METHODS OF SECURING WAGE DATA

Before discussing the significance of the wage figures given in Tables IV, V, and VI, it may be well to give a brief description of the methods followed in gathering and compiling the data for each table, and to compare the results secured from each. The sample-data method,

used in obtaining the material for Table IV, consists in getting as accurate information as possible from a limited number of cases selected at random from the whole number, the idea being that this limited group or "sample" will be representative of the whole body, and that therefore the things which are true of the sample will be approximately true of the whole group. If the sample is sufficiently large and sufficiently representative, the averages or other statistical expressions derived from it will approximately equal similar ones derived from the complete data. The advantage of this method is that it is inexpensive because it avoids the vast amount of work necessary to gather and compute the complete data. An investigation by this method may include many more details, because with only a fraction of the actual cases to handle, the analysis may be much more nearly complete. The danger is that the sample may be too small or may represent only a part of the cases. The data may be gathered by an enumerator who goes personally to those having the facts, or it may be secured through correspondence by mailing a schedule of inquiries to the informants to be filled out and returned.

The estimate method, which is the basis of Table IV, consists in securing from a limited number of persons, presumed to be familiar with the facts, their judgment as to these facts, either in absolute figures or in terms of percentage of change from conditions as they existed in the past or exist in some other locality. It is by this method that the Bureau of Crop Estimates of the United States Department of Agriculture gets practically all its figures on the acreage, yield, and value of crops and the number and value of livestock. It has the advantage of being very inexpensive, and has generally been regarded as the only practical method by which to obtain figures on such a large number of items so frequently and for such a large area as is undertaken by the Bureau of Crop Estimates. It has the disadvantage of yielding figures based on no actual cases, but on the estimates of persons as to what the usual or representative conditions are.

The third method is that followed by the United States Census Bureau, the various state census authorities, and those employed to make enumerations of property for purposes of taxation. It is necessarily very expensive and for this reason is usually restricted to the gathering at rather infrequent intervals of a few general data on matters of interest to a large number of people, like the federal and state census data, or to the getting of facts such as must be known for each individual, as for the purpose of taxation. For these reasons it does not lend itself well to the securing of facts in minute detail. The information is secured by enumerators who fill in a printed schedule of inquiries for each informant and who visit all persons within the given political unit. Table VI is based on this sort of enumeration.

TABLE VII

Comparison of Farm Wage Averages for 1919 as Secured by Three Methods of Inquiry

Area	Average monthly wage for year contracts, as secured by			Average monthly wage for summer as secured by		Average monthly wage for winter as secured by		Average daily wages for harvest work, as secured by		Average daily wages for other work, than harvest work, as secured by	
	Sample data	Estimates	Census	Sample data	Census	Sample data	Census	Sample data	Estimates	Sample data	Estimates
State	$55.00	$54.00	$54.00	$58.00	$60.00	$36.00	$42.00	$4.75	$4.50	$3.00	$3.50
Section I	57.00	57.00	52.00	59.00	58.00	28.00	40.00	5.00	5.00	3.00	3.75
Section II	54.00	51.00	54.00	58.00	61.00	38.00	40.00	4.25	4.00	3.00	3.25
Section III	53.00	52.00	52.00	57.00	59.00	34.00	39.00	4.75	4.75	3.00	3.50
Section IV	55.00	55.00	56.00	61.00	63.00	46.00	43.00	5.00	4.75	3.50	4.00
Section V	55.00	58.00	52.00	56.00	58.00	38.00	39.00	4.25	4.50	3.00	3.75
Section VI	56.00	52.00	56.00	55.00	61.00	38.00	45.00	4.00	3.75	3.25	3.00
Section VII	56.00	52.00	62.00	54.00	64.00	42.00	57.00	4.00	3.50	3.00	3.00

Since the data in the foregoing tables are not in completely similar terms, it is impossible to make a thoro comparison of results. However, in Table VII, the more important wage contracts are compared, the figures being taken from Tables IV, V, and VI, and arranged in parallel columns.

The figures for the state as a whole on wages by the month for men hired for the entire year,[5] the only wage contract for which figures are available from all three sources, are very nearly identical. There is a rather close agreement in them for the various sections of the state as well, but also some very marked disagreements. For example, for Section I, the leading small grain area of the state, the census figure is $5 lower than in the other two. The best explanation of this seems to be that in parts of this area many children are employed for picking up potatoes, and the lower wages paid for this sort of work seem to have figured so largely in the average as to reduce it far below the normal level for ordinary farm labor for the section.[6]

Much of this sort of labor was reported on the schedules of the sample-data survey, but in compiling the data these returns were excluded in an effort to make the averages representative of the wages of mature farm laborers without managerial responsibility who are engaged in the usual farm work of the region. Hence figures representing the wages of children as well as of hired farm managers and specially skilled laborers were excluded.

There are discrepancies also in Sections II, V, VI, and VII. In three of these four cases, the estimated figure is lower than the others. This is a tendency manifested throughout all the tables and is difficult to account for except on the grounds that the estimators, giving figures based on their judgment rather than on actual experience, endeavor to be conservative in their estimates, particularly in a time when wages are rising. However, the most important divergence is the census figure for Section VII, which is $6 above the sample-data average and $12 above the estimated average. It is to be explained largely in the nature of the work for which wages by the month are paid. This section embraces most of the forested and cut-over region of the state. The typical farm business unit is small, profits are low, and the bulk of the labor, as indicated in Table II, is hired by the day at wages lower than those obtaining in other parts of the state. The few men working by the month and reported to the census takers are probably serving as farm

[5] The census figures given in this part of the table were derived by averaging the summer and winter wages as given in Table VI. As these summer wages as reported probably covered for the most part the eight months of the open season, they were given double weight in the averages.

[6] The census figures for summer wages in Clay County show nearly four times as many hirings in proportion to the number of farms as do those in the neighboring counties, and the average wage rate was only about half as high.

managers or in some capacity carrying more responsibility and higher wages than does ordinary farm work. Many of them are doing timber or road work. A monthly average including all the cases existing, like the census average, will give figures higher than in a region where most of the men are hired to do ordinary work. Here again in compiling the sample data, all returns were excluded which indicated that the men were functioning as something other than ordinary farm laborers.

In the second part of Table VI, the sample-data figures representing the average of wages paid men for the active farm season, that is, from about March 15 to November 15, are set in comparison with the census averages of "summer" wages, it being assumed that the farmers would report wages for the season in answer to this question in contrast to "winter" wages paid during the cold weather, largely for labor in the care of livestock. No estimate figures are available for 1919 on this type of contract. According to the sample-data returns, as indicated in Table II, this is the most common type of month contract in the state. The most noticeable difference shown in this comparison is the consistently higher level of the census averages. They are in general from $2 to $3 higher than the corresponding sample-data averages.[7] The reason for this seems to be that many farmers hiring help only for the latter part of the season hired by the month rather than by the day and at a much higher wage per month than they would have paid if hiring for the entire season. In many cases, also, men hired for the season were given a higher monthly wage as the season advanced. These high monthly wage figures for the latter part of the season were undoubtedly reported as "summer" wages in the state census, and being included in the averages, raised them somewhat above the normal level for full season pay. In compiling the sample data, the wages covering the first half of the season and those covering the last half were averaged by themselves, as reported in Tables II and IV. When these differences and their causes are taken into account, the figures on month wages on season contracts agree very closely.

The sample-data returns on winter wages were too meager to give representative averages. (See Table II.) There were nearly 12,000 census returns on winter wages, but many of these, as already explained, represented year contracts with uniform wages per month throughout the year. In some cases they represented winter wages of managers or farm foremen hired by the year. Not only is their general level too high, but it is especially high in certain sections. In Section VII, for example, it includes wages of men hired by settlers to help them get out their pulpwood and timber.

[7] The explanations already given of the low average in Section I and high census averages in Sections VI and VII, explain the two exceptions.

The state census blanks contained no questions on the rates of day wages. The sample data and estimate returns correspond very closely as to harvest wages even by sections. The estimated averages are, except in two sections, a little lower than the sample-data average. An explanation for this has already been suggested. The results of such comparisons as can be made on the basis of the figures available in this investigation indicate that estimates normally run lower than the actual figures in all instances in which identical cases are involved. Day wages for other than harvest work, on the other hand, show higher averages from the estimates than from the sample data. The reason for this is that the two averages are not strictly comparable. In the sample-data schedule, the farmer was asked to report the specific task for which the men were employed. In making up the tables from these returns, the wages paid for threshing, stacking, silo filling, and haying, if done at a time of the year when it would have to compete for labor with these other lines, were included with those for strictly harvest work as belonging to the same general class. Under the term "other labor" were grouped such tasks as early season haying and miscellaneous farm work. Very probably many of the correspondents of the Bureau of Crop Estimates interpret the term "harvest" narrowly and base their estimate of wages for "other labor" very largely on lines of work which carry wages almost if not quite as high as harvest work.[8]

The foregoing comparison of results throws some light, at least indirectly, on the relative merits of the three methods of collecting farm wage data. It would seem that the census method, while furnishing valuable checks on some of the results of the other methods, does not lend itself to detailed inquiries on complicated questions such as farm wages. If enough questions are included to bring out the details accurately, the method becomes too expensive. It is therefore best suited to collecting data on a few general, simple, and outstanding points.

Many of the details included in the sample-data schedules could be put into an estimates schedule. For many of them, however, estimates would not do, for example, the matter of specifying the dates between which each man was employed. And yet this was the basis of a large and important part of the analysis of the sample-data figures. Certainly no adequate equivalent of these facts could have been obtained through estimates of any sort. Further, it is reasonable to suppose that a more accurate average can be obtained by using actual data than by using estimates. The correspondent ordinarily bases his judgment as to "usual" or "average" conditions entirely on general impressions. He seldom has

[8] It is not to be concluded that the estimates on all sorts of data are likely to be uniformly lower than the actual figures. On the contrary, there is reason to believe that on such things as crop yields, acreage of the various crops planted, and number of livestock, the estimates are as likely to be too high as too low.

data enough even for a hasty analysis of wage distribution. If the estimates are numerous, and those that are too high are counterbalanced by others that are too low, the final result will be representative; but there is no guarantee that this will be true. In the case of actual data, the truth of the averages depends alone on the adequacy of the sample taken.

It is in this direction that the weakness of the sample-data method lies. If the facts are collected by enumerators who visit the farmers personally, the method is very expensive, especially if a good many details are included. As a result, the schedules are usually sent by mail. This introduces two difficulties: (1) many correspondents misinterpret the inquiries and give useless answers, and (2) many farmers do not wish to be troubled with the matter and refuse to fill and return the schedules. The first difficulty can be overcome by carefully framing the questions, and the second by sending out enough schedules. In the case of the sample data used in this discussion, approximately 7500 schedules were mailed, of which something less than 20 per cent were filled and returned. About 1500 of the returns were usable.

The question arises as to how the investigator using this method will know whether his sample is large enough to be representative. The best test of this is what is termed the frequency distribution of the data. While there is considerable variation in any data, such as the wages paid to all the hired men of a certain class in a specific year, most of those hired will receive nearly equal wages, and the wages most frequently paid will be near neither the lower nor the higher limit, but will tend to be near the middle of the range. From this largest group near the middle, the numbers hired at the various levels above and below decrease regularly so that at the very highest and the very lowest levels only a very few hirings occur. The larger the number of cases taken into account, the more nearly regular this distribution becomes, and the more regular the rise and decline. All that is necessary, however, is to have a large enough sample to show a reasonably regular frequency distribution. A sample that is too small to show this is an inadequate basis on which to judge the whole volume of data; therefore averages or other representative figures based on it are almost sure to be misleading. It must be admitted that in the case of certain wage contracts, such as those hiring for winter and for the first half of the season, the data obtained from the schedule in question are too few to make a good sample, particularly with reference to the individual sections. But in the case of the more important contracts the samples seem to be adequate.

WAGE RATES BY SECTIONS OF THE STATE

Wages of farm labor vary considerably in different sections of a given state, with different times in the year in the same locality, and with the different kinds of work for which the laborers are hired. They vary from region to region because of differences in the productivity of the land, in the efficiency of the farmers who are hiring labor, in the kind of work for which most of the men are hired, and in a great variety of economic and social conditions which affect locally the supply of labor and the demand for it. If labor moved freely from section to section in response to differences in wages, naturally wage levels would be the same everywhere. But farm labor is not very mobile. Supplied as it is largely from young men reared on the farm, it does not flow readily to other localities where wages are higher unless the difference in wages is fairly large. Consequently the farmers in the better farming districts may bid wages considerably above the level of the poorer districts without attracting much additional labor. Hence profitable farming in any section may mean higher wages in that section. Profitableness in farming depends primarily on the productiveness of land and the managerial ability of the farmers. Since in the long run the more able operators tend to get possession of the best natural resources, these two influences are usually found in combination. Differences in the kind of farm work affect wages because some kinds of farm work, such as dairying, require more skill and higher qualities than others, such as crop work; and other things being the same, wages may vary between localities according to the extent that one kind of work or another predominates. However, if local conditions make for an abundance of this superior skill and these higher qualities, the wages of the men possessing them may be lower than those of the laborers in another region whose work is not so exacting but who are not so numerous relatively to the demand for their services.

Our statistics indicate that there were regional variations in 1919 in the wages of Minnesota farm labor, tho the variations were not extreme. Figure 5 gives these variations by sections of the state for summer season help hired by the month, and for harvest hands hired by the day. The figures given are based on the sample data. Tables IV, V, and VI, or the consolidated figures of Table VII, show that these variations are fairly consistent for both month and day wages. Wages are highest in Sections I and IV, which together comprise the western part of the state. Probably the averages best reflecting the conditions of wages by the month are those of the sample data on wages of men hired for the season. These show month wages to be highest in Section IV, which, it will be recalled, has a type of agriculture based on corn, livestock, and small grain. Farms are large here, land values are the highest in the state, and farming is generally profitable. The next

highest average is found in Section I, the leading small grain area, where the natural conditions are not quite so favorable but where the size of the farm business is large and the type of farming such as to make a strong demand for labor in the open farming season. Next in order come Sections II and III which, tho small grain areas so far as cropping is concerned, are of great importance in dairying. As indicated by this set of averages, the regional variations in wages seem to bear a closer relation to the relative profitableness of farming and the size of the farm business unit than to any other factors.
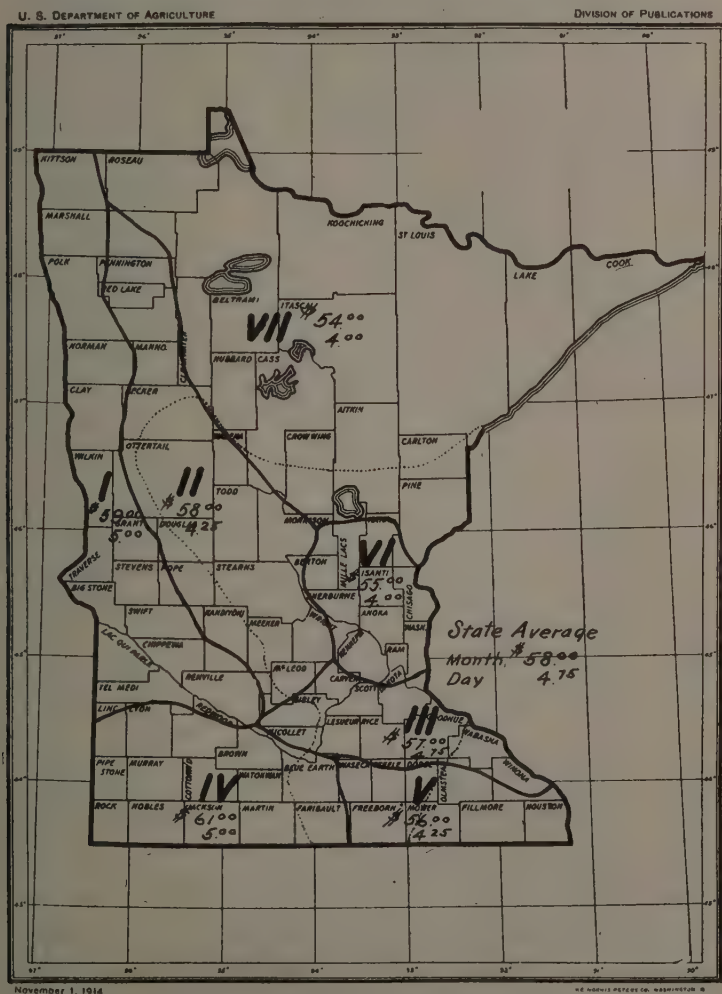
Fig. 5. Average Monthly Wage of Farm Labor in Minnesota, Hired for the Summer Season; Also of Harvest Labor Hired by the Day, 1919 (Sample data)

The best indexes of day wages are of course the averages for har-
vest labor, which in the case of the sample data cover wages paid for
threshing, stacking, and other kinds of special work coming during the
rush period of the crop season.   Variations in these wages are evidently
due to different degrees of intensity of demand for labor of this tempo-
rary sort. Such wages are highest in Sections I and IV, not only because
of the importance of small grain which requires such a large amount
of labor during the latter part of the season, but also because the farm
business is so large that the excess of "peak load" labor over that of the
earlier part of the season is so great that more help is needed of this
sort than in the areas of smaller farms.   The greater importance of
corn in Section IV than in Section II and III evidently does not modify
the seasonal distribution of labor sufficiently to counteract the effect
of the large acreage of small grain per farm.   In Sections VI and VII,
where small grain is least important and where the farm business is
small, the average for this class of wages is the lowest in the state.

Table VIII combines the returns obtained by the three methods.
The figures given, in the writer's opinion, fairly represent the wage
rates actually paid in 1919 in the several sections of the state for the
more important classes of contracts.   For the most part the figures
are identical with those secured by one or the other of the methods
which seem to give the most reasonable results.   In a few cases, the
figure has been approximated.

TABLE VIII

Approximate Wages of Farm Laborers in Minnesota, 1919

	State	Type-of-farming sections						
		I	II	III	IV	V	VI	VII
Year	$55.00	$57.00	$54.00	$53.00	$56.00	$55.00	$56.00	$56.00
Season	58.00	59.00	58.00	57.00	61.00	57.00	56.00	55.00
Winter	38.00	36.00	38.00	36.00	40.00	38.00	38.00	42.00
Harvest* ...	4.75	5.00	4.25	4.75	5.00	4.25	4.00	4.00
Other*	3.00	3.00	3.00	3.25	3.50	3.00	3.25	3.00

* Day wages.

WAGE RATES BY SEASONS

The most marked variations in wage rates are the seasonal ones.
Variations of this sort result almost entirely from two causes: (1) farm
work in all parts of the year or season is not equally important from the
point of view of returns.   If work which brings a low return is done
at all, the farmer will pay lower wages to have it done than he will for
work bringing high returns.   (2) The amount of work, and hence the
demand for labor, varies greatly in different parts of the year or season.

These seasonal variations are revealed in the monthly wage statistics
in two ways.   The monthly wage paid over a long period, which includes

the slack intervals, is lower than that paid for a short period covering the busiest part of the year. The average monthly rates for laborers hired by the year, given in Table IV, are lower for the state and for almost all sections than for laborers hired for the season. Again, laborers hired by the month for short periods receive greatly different wages, depending on the time of year. Winter wages are invariably low. Wages for the early part of the season, in Table IV, average only $53, while those for the second half average $71. So little farm work can be carried on in the winter that the demand is very light, and frequently the enterprises which require winter labor beyond what the farmer can do himself add less to the gross income of the farm than those requiring work at rush seasons. In the spring the nature of the work is such as to make a relatively light demand for man labor, while the tasks beginning with midsummer require a large amount of man labor, making the demand very heavy and the wages high.

Seasonal variations in the day wage rate are well brought out in Table IX. Here the portion of the working season from May 4 to October 26 is divided into one-week periods for the purpose of determining the relative amount of day labor at the different wage levels, and the average daily wage in the different parts of the season. The figures in the first column, headed "Wage classes," indicate the limits within which the wages fall which are listed respectively on each horizontal line. These limits are so selected that their means are the even-dollar quantities, two, three, four, etc. The figures in the body of the table represent the number of weeks of work reported for each specific week for each wage level. Since 76 per cent of the weeks of work represented in the table was paid for at some even-dollar rate, these classes represent substantially the even-dollar rates from $2 to $7, respectively. Each column in the body of the table is thus a frequency table for a specific week showing the number of man-weeks of work paid for in that particular week at each wage level so far as reported in the sample data. This enables us to determine at a glance what was the representative or most frequent wage paid during that week. The figures at the bottom show the total number of "weeks of work" reported for each week and also the average of all wages reported for each week. The last column shows the number of weeks of work paid for at various wages for the entire period.

The lower section of the table gives the average wages by weeks for six of the seven sections of the state. The rates at different periods clearly reflect the differences in systems of farming. The "peak load" is much more pronounced in Sections I and IV than in the other sections.

TABLE IX

RANGE OF WAGES PAID FARM LABORERS IN MINNESOTA WORKING BY THE DAY, BY WEEKS FROM MAY 4 TO OCTOBER 25, 1919

Number of weeks of work reported at the several wage levels for weeks beginning

Wage classes	May				June					July			
	4	11	18	25	1	8	15	22	29	6	13	20	27
$1.50–$2.49	12.0	12.0	14.0	14.0	11.0	11.0	10.5	11.0	19.0	7.0	7.5	6.5	5.5
2.50– 3.49	34.5	39.0	39.5	34.5	36.0	39.0	43.0	44.5	63.0	69.0	71.0	62.5	57.0
3.50– 4.49	15.0	14.0	6.5	12.0	17.0	18.0	18.0	18.0	33.0	55.5	66.5	70.0	73.0
4.50– 5.49	2.0	2.0	2.0	2.0	5.0	5.0	5.0	7.0	16.0	33.5	48.5	63.0	77.0
5.50– 6.49	...	...	...	...	...	...	...	...	3.0	6.0	10.5	12.0	17.5
6.50– 7.49	...	...	...	...	...	...	...	...	...	1.0	1.0	1.0	1.5
All classes	63.5	67.0	68.0	62.5	69.0	73.0	76.5	80.5	135.0	172.0	205.0	215.0	231.5
Average wage	$2.96	$2.94	$2.86	$2.89	$3.11	$3.10	$3.10	$3.11	$3.56	$4.14	$4.15	$4.19	$4.14

Average wages by type-of-farming sections

Sections	May				June					July			
	4	11	18	25	1	8	15	22	29	6	13	20	27
Section I	$2.75	$2.86	$2.86	$2.94	$3.01	$3.16	$3.17	$3.41	$4.04	$4.18	$4.27	$4.42	$4.65
Section II	2.50	2.50	2.50	2.53	2.87	2.92	2.92	2.95	3.35	3.41	3.48	3.58	3.81
Section III	2.90	2.90	3.00	3.00	3.13	3.25	3.25	3.30	3.83	3.92	3.96	4.08	4.17
Section IV	3.05	3.05	3.45	3.50	3.50	3.54	3.40	3.41	3.73	3.92	4.03	4.35	4.59
Section V	3.00	3.00	3.25	3.25	3.26	3.15	3.14	3.14	3.36	3.47	3.62	3.60	3.67
Section VI	2.86	2.86	2.88	2.88	3.02	3.10	3.10	3.25	3.30	3.30	3.28	3.30	3.35

TABLE IX—*Continued*

RANGE OF WAGES PAID FARM LABORERS IN MINNESOTA WORKING BY THE DAY, BY WEEKS FROM MAY 4 TO OCTOBER 25, 1919

Number of weeks of work reported at the several wage levels for weeks beginning

Wage classes	August					September				October			All weeks
	3	10	17	24	31	7	14	21	28	5	12	19	
$1.50–$2.49	4.0	4.0	3.0	2.5	4.0	4.0	4.0	3.0	2.5	3.0	4.0	3.0	171.0
2.50– 3.49	52.5	51.0	46.0	45.0	33.0	33.0	39.0	38.5	31.0	28.5	27.0	25.0	1082.0
3.50– 4.49	66.0	65.0	68.5	62.0	36.5	33.0	21.5	19.5	15.0	18.5	21.0	16.5	867.5
4.50– 5.49	113.0	115.5	97.5	73.0	60.0	48.0	40.5	36.0	25.5	19.0	16.5	16.0	954.0
5.50– 6.49	26.0	23.5	22.0	20.0	16.5	13.5	10.5	6.0	3.0	2.0	1.0	1.0	288.0
6.50– 7.49	2.0	2.0	1.5	1.0	2.0	2.0	1.0	...	...	...	...	...	72.0
All classes	263.5	262.0	236.5	214.5	152.0	143.0	116.5	103.0	77.0	71.0	70.0	62.5	3434.5
Average wage	$4.34	$4.32	$4.30	$4.29	$4.28	$4.27	$4.05	$3.93	$3.86	$3.75	$3.70	$3.77	$4.09

Average wages by type-of-farming sections

Sections	3	10	17	24	31	7	14	21	28	5	12	19	All weeks
Section I	$4.84	$4.86	$4.86	$4.90	$4.86	$4.81	$4.67	$4.57	$4.30	$4.09	$4.05	$4.05	$4.43
Section II	3.92	3.90	3.90	3.92	3.89	3.83	3.83	3.67	3.54	3.43	3.40	3.40	3.49
Section III	4.54	4.32	4.23	4.19	4.18	4.06	3.78	3.64	3.69	3.81	3.83	3.83	3.97
Section IV	4.72	4.59	4.52	4.38	4.31	4.36	4.50	4.52	4.53	4.45	4.45	4.45	4.25
Section V	3.74	3.75	3.77	3.75	3.75	3.55	3.54	3.59	3.81	3.90	3.90	3.95	3.59
Section VI	3.51	3.55	3.57	3.57	3.20	3.19	3.23	3.18	3.23	3.29	3.29	3.34	3.22

Wages hold up much better late in the season in Sections IV, V, and VI than in the other sections. This is because of the corn crop in Sections IV and V, and because of the potato crop in Section VI. In Sections III, IV, V, and VI there is a somewhat slack period between the small-grain and the corn harvesting. In the southern sections, there is evidence of a little slackness about the middle of June, between the corn planting and the haying and harvesting. In all the sections, the abrupt rise in wages comes in the first and second weeks in July. The very highest wages are paid in the first part of August in the southern sections and a week or two later farther north. It must be stated that in some cases these averages may not be fairly representative. In some weeks in some sections, only a few hirings were reported. This is especially true in May and October.

A comparison of the total figures for weeks of work and the average daily wage, as given at the close of the first section of the table, shows a very close correlation between the amount of labor hired and the average of the wages paid. The amount of labor hired by the day increases with considerable regularity up to the week of August 3-10, and from that date on decreases with equal regularity. The average of the wages rises and falls with equal regularity and reaches its highest point at the same date with the maximum amount of hiring. This is even more true by sections than for the state as a whole. This would seem to show conclusively that the amount of labor demanded has a most important influence on the wage level.

It is of interest here to compare by weeks the most usual wage, as indicated in the body of the table, with the averages. For seventeen out of the twenty-five weeks covered by the table, the wage of most frequent occurrence was $3, but the average during these same weeks ranged from $2.86 to $4.15. The amount of difference between the average and the most frequently occurring wage depends, of course, on the number of hirings at wages either considerably above or considerably below the wage of greatest frequency. In the case of the data given in this table, probably the average is a better representative of the general wage conditions than the wage of most frequent occurrence, since it reflects with greater accuracy the effect of changes in demand for labor upon the wages that farmers must pay. However, the averages themselves without the detailed distribution as given in the table would present but an inadequate picture of the real situation regarding day wages.

WAGE RATES BY KINDS OF WORK

To test the relation of the kind of work done to the day wages paid, Table X was constructed. Not so many cases could be included in this tabulation because the particular work for which the men were hired was less frequently specified in the schedules than the dates of their employment.

TABLE X

RANGE OF WAGES PAID FARM LABORERS IN MINNESOTA WORKING BY DAY AT SEVERAL KINDS OF WORK, SEASON OF 1919

Wage classes	Number of weeks' work reported at the various wage levels for different kinds of work							
	Haying	Har-vesting	Stack-ing	Thresh-ing	Silo filling	Potato picking	Miscel-laneous	All kinds
$1.50–$2.49	5	1	..	1	1	1	80	89
2.50– 3.49	53	22	3	14	6	9	191	298
3.50– 4.49	66	78	14	45	29	18	118	368
4.50– 5.49	46	151	20	129	33	8	71	458
5.50– 6.49	1	17	3	24	2	6	22	75
6.50– 7.49	..	1	..	5	1	1	3	11
All classes......	171	270	40	218	72	43	485	1299
Average wages..	$3.76	$4.49	$4.43	$4.77	$4.36	$4.21	$3.41	$4.03

This study shows that the kind of work in itself has relatively little influence on the day wages paid. There are no significant differences in the wages paid for harvesting, stacking, threshing, and silo filling, all of which tasks come during the part of the season in which there is a maximum demand for labor. The most frequent wage for all of these groups is the same. The averages for haying and potato picking are appreciably lower than for the other kinds of work, but both of these two classes represent work done for the most part at times of the year when the demand for labor is not so heavy. There are, to be sure, certain kinds of work done in connection with farming which bring higher pay than ordinary tasks, regardless of the season. Operating traction engines and grain separators, carpentry and masonry and tile laying are examples. However, few cases of hiring for tasks of this class were reported in the schedules and these were excluded in compiling the data. It seems evident that, as compared with seasonal wage variations, differences in wages with different kinds of work are of very minor importance and that the demand for labor, as it rises and falls during the season, is the major influence behind wage differences.

TABLE XI

WAGES (WITH BOARD) OF FARM LABOR IN MINNESOTA AND BORDERING STATES, 1866–1920

Year	Month					Day—Harvest work					Other day work				
	Minnesota	Iowa	Wisconsin	North Dakota	South Dakota	Minnesota	Iowa	Wisconsin	North Dakota	South Dakota	Minnesota	Iowa	Wisconsin	North Dakota	South Dakota
1866	$14.85	$13.28	$13.99	...	$14.08	$1.60	$1.32	$1.51	...	$1.41	$0.95	$0.84	$0.90	...	$1.06
1869	13.17	13.12	13.56	...	...	1.73	1.64	1.44	...	...	0.87	0.83	0.84	...	...
1875	14.20	13.98	14.28	...	17.79	2.00	1.82	1.67	...	1.65	0.93	0.88	0.87	...	0.94
1878	15.53	13.82	13.73	...	16.47	2.24	1.56	1.69	...	...	0.93	0.80	0.79	...	0.91
1880	16.33	13.74	14.76	...	18.10	2.44	1.57	1.57	...	1.97	1.03	0.86	0.83	...	0.99
1881	16.44	16.38	15.87	...	19.55	2.29	1.69	1.67	...	2.15	0.99	0.92	0.90	...	1.27
1882	17.75	17.95	17.90	...	...	2.16	1.81	2.10	...	2.19	1.02	0.99	0.99	...	1.11
1885	16.75	17.00	16.78	...	17.60	1.89	1.61	1.57	...	1.00	0.99	0.97	0.95	...	1.08
1888	17.68	17.34	16.80	...	18.21	1.75	1.46	1.44	...	1.64	1.00	0.97	0.97	...	1.10
1890	16.60	17.00	16.75	...	17.10	1.51	1.50	1.30	...	1.52	0.98	0.95	0.87	...	1.04
1892	17.60	17.75	17.00	21.00	18.25	1.70	1.40	1.38	1.70	1.60	1.00	0.98	0.88	1.20	1.06
1893	18.78	19.46	18.58	22.27	20.24	1.56	1.33	1.27	1.73	1.57	1.02	1.00	0.96	1.13	1.11
1894	16.03	17.90	16.74	18.80	16.73	1.24	1.16	1.12	1.40	1.13	0.84	0.88	0.85	0.94	0.81
1895	17.32	18.15	16.92	19.47	16.89	1.46	1.19	1.11	1.60	1.37	1.00	0.93	0.84	1.03	0.96
1898	18.16	18.18	17.50	20.10	18.90	1.55	1.28	1.22	1.68	1.61	1.01	0.99	0.93	1.04	1.11
1899	19.98	19.32	19.20	21.82	20.41	1.84	1.47	1.40	1.99	1.87	1.18	1.11	1.06	1.18	1.26
1902	22.79	22.14	22.17	25.05	23.55	2.04	1.75	1.61	2.18	2.08	1.31	1.24	1.14	1.30	1.36
1906	25.81	24.69	25.83	28.90	27.82	2.22	1.93	1.78	2.48	2.32	1.46	1.38	1.35	1.51	1.60
1909	28.30	28.14	24.39	32.33	30.38	2.23	2.08	1.79	2.58	2.38	1.53	1.53	1.35	1.66	1.69
1910	26.00	28.00	26.00	29.00	27.00	2.23	2.12	1.76	2.40	2.35	1.48	1.57	1.35	1.60	1.54
1911	26.10	28.30	26.20	28.90	27.00	2.26	2.07	1.75	2.36	2.08	1.53	1.58	1.37	1.60	1.50
1912	27.90	29.60	27.40	30.30	28.60	2.37	2.16	1.85	2.70	2.40	1.59	1.66	1.46	1.91	1.65
1913	28.90	30.70	28.10	31.00	30.00	2.43	2.25	1.93	2.70	2.37	1.67	1.70	1.46	1.85	1.69
1914	28.70	30.10	28.00	31.20	30.10	2.36	2.24	1.87	2.68	2.40	1.66	1.67	1.45	1.75	1.71
1915	28.80	31.10	28.50	32.00	31.20	2.33	2.20	1.83	2.82	2.47	1.65	1.68	1.45	1.80	1.71
1916	33.00	34.10	31.00	33.20	33.70	2.55	2.35	2.02	2.90	2.69	1.85	1.85	1.66	1.94	1.90
1917	39.00	41.00	36.00	41.00	42.00	2.96	2.83	2.43	3.40	3.30	2.17	2.23	2.00	2.45	2.52
1918	47.10	50.00	43.50	52.00	55.70	3.90	3.65	3.00	4.50	4.40	3.00	2.90	2.48	3.20	3.50
1919	53.70	55.00	48.70	56.00	65.00	4.30	4.46	3.39	4.85	4.95	3.32	3.46	2.90	3.50	3.90
1920	67.00	66.35	62.00	70.00	76.00	5.10	5.00	4.15	6.10	5.50	4.15	4.08	3.50	4.40	4.65

WAGES AS RELATED TO OTHER FARM EXPENSES

It is worth while now to consider farm wages in relation to the other expenses of production, such as rent and cost of equipment. Have wages risen more or less rapidly than these other expenses? What has been the effect of these changes on the amount of labor used? This part of the bulletin tries to answer some of these questions.

THE COURSE OF FARM WAGES

The United States Department of Agriculture since 1866 has secured estimates on the wages of farm labor from its correspondents and published the results in the form of state averages. Prior to 1909 these figures were collected at rather irregular intervals, but since then they have been collected annually. Table XI gives the Minnesota averages for this whole series of wage surveys together with those for Wisconsin, Iowa, South Dakota, and North Dakota.

If the figures of this table fairly approximate wages on farms of this region throughout the period, month wages almost doubled between 1866 and 1909, and more than doubled again between 1909 and 1920. Day wages in harvest have not increased so rapidly. Up to 1913, in Minnesota, they had never been 50 per cent above the 1866 level, and in 1920 they were only a little more than three times as high. Practically throughout the entire period, farm wages both by month and by day were higher in Minnesota than in Wisconsin and Iowa, and lower than in the Dakotas. This seems to indicate that wages are normally higher in the newer portions of the country, especially prairie regions, than in the older and better developed portions.

The more rapid increase in month wages as compared with day wages indicates that the demand for labor throughout the season has increased more rapidly than for labor needed only a short time for special work. Such a relative increase in the all-season demand for labor may be expected to accompany the growth and development of farming in any new country.

CHANGES IN PRICES OF THE OTHER FACTORS OF PRODUCTION

Great as has been the increase in the wages of farm labor, the prices of most of the other factors of agricultural production have, throughout the period, except in the last few years, risen even more rapidly. Table XII shows both the actual and the relative change in the average value of land per acre including improvements, the average price of work horses, the aggregate price of a representative group of farm imple-

ments,[9] and the average monthly wages of farm labor; for each of the census years from 1880 to 1920.[10] The prices of these things are taken for comparison because they represent the Minnesota farmer's most important expense items, his outlay for land, labor, equipment, and power.

TABLE XII

CHANGES IN VALUES OF FARM PROPERTY AND IN WAGES OF FARM LABOR IN MINNESOTA, 1880–1920

Date	Values				Percentage of change from 1880			
	Land, per acre	Horses, per head	Machinery, per representative group	Wages, per month	Land, per acre	Horses, per head	Machinery, per representative group	Wages, per month
1880	$14.45	$64.58	$560.00	$16.33	100	100	100	100
1890	18.22	77.92	447.00	16.60	126	121	80	102
1900	25.51	67.90	378.00	19.98*	177	105	68	123*
1910	46.62	132.16	565.00	28.30†	323	205	101	173†
1920	109.25	96.48	1056.00	53.70‡	756	149	189	328‡

| * For 1899. | † For 1909. | ‡ For 1919. |

In the second half of Table XII the prices existing in 1880 have been taken arbitrarily as 100 per cent. The difference between 100 and the percentage figure appearing for any other year will therefore represent the percentage of change in price since 1880. The comparison thus obtained shows that with the exception of farm machinery the increase in the price of labor prior to the late war was less than for any other item. While wages increased only 73 per cent by 1910, the price of horses increased 105 per cent, and the price of land 223 per cent.

In most cases these price changes have been very closely related to changes in the general price level for the whole country. In Figure 6 this general price level is represented by United States Bureau of Labor Statistics price indexes, which are based on averages of the wholesale price for the United States of a large number of commodities, and are expressed as relatives based on the figures for 1914. On the same chart

[9] This group consists of one each of the following: farm wagon, corn plow, gang plow, grain drill, harrow, twine binder, and mower. Figures were secured from wholesale dealers supplying Minnesota local dealers. For the purpose of comparing changes in prices of machinery with changes in the price of land, horses, and labor, what is needed is a representative rather than a complete list of equipment. Wholesale prices probably indicate changes in retail prices with sufficient accuracy.

[10] The period 1880-1910 was selected as being best for comparative study. The figures for 1920 have become available since the study was made and have been added to the table. The year 1880 is taken for the beginning because conditions were then relatively stable, and it also marks the point at which farming had become fairly established over most of the productive portion of the state.
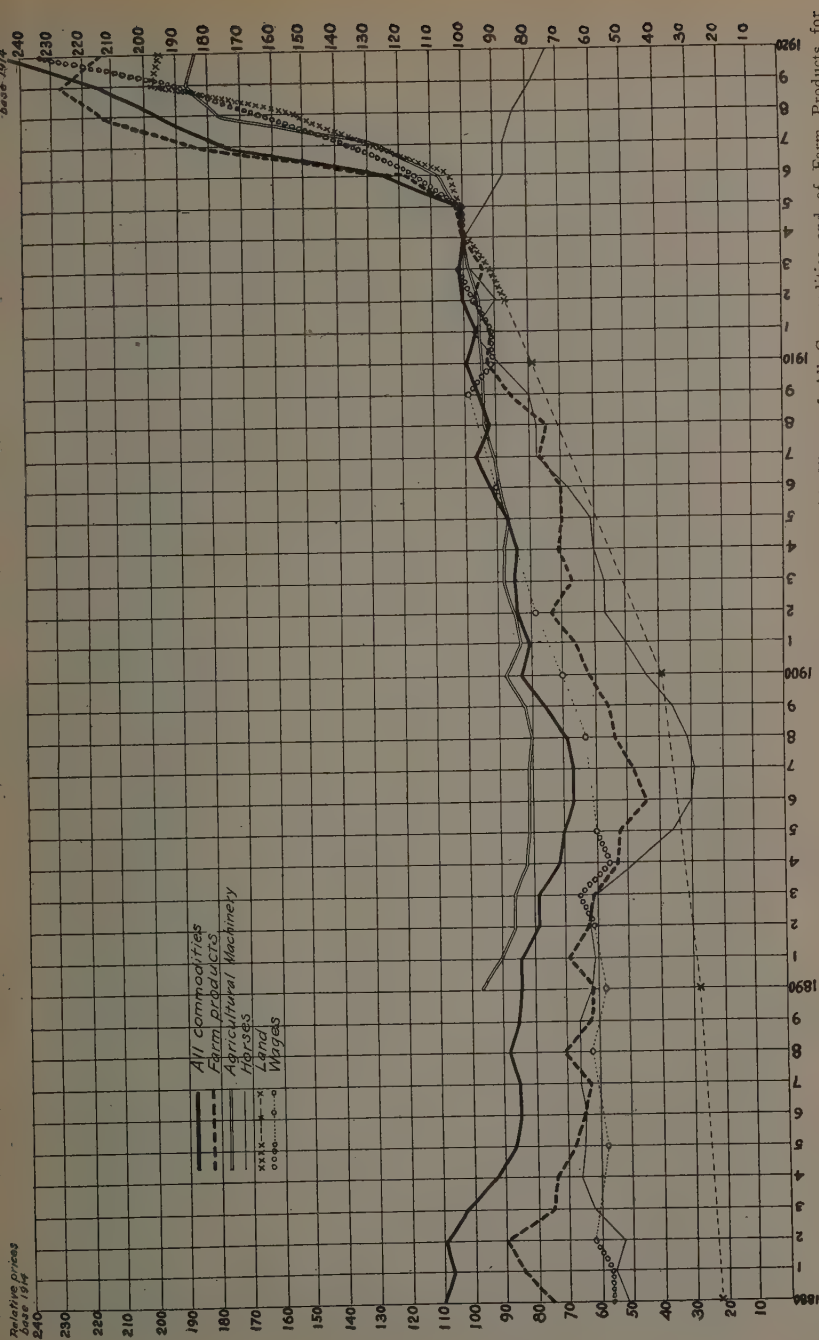
Fig. 6. Relative Prices of Selected Factors of Agricultural Production in Minnesota Compared with Those of All Commodities and of Farm Products for the United States, 1880-1920

The base year for all prices is taken as 1914. In interpreting any chart of "relative" prices, that is, prices given in terms of percentages of the prices of the base year, it is important to understand that divergence of the curves means simply differences in the rate of change.

is placed a curve for farm products for the country as a whole, and
other curves for the Minnesota prices of those factors of farm produc-
tion already discussed, in so far as comparable figures could be obtained.

It will be noted from this chart that the trend of the general price
level was gradually downward from 1880 to about 1896. This is a
part of the long period of price decline dating from near the close of
the Civil War. From 1897 to 1915 the trend was gradually upward,
followed by the extremely rapid price increases of the World War
period. The curve representing the general average prices of agricul-
tural products stays very much below the curve of all commodities in
the early part of the period, approaches it more closely after the low-
price point of the middle nineties, and actually stands above it for
nearly every year from 1914 to 1919. This means simply that the
prices of agricultural products have been rising somewhat more rapidly
during the last twenty-five years than the prices of other commodities.
This indicates that prior to that period, relatively more people were pro-
ducing agricultural commodities than since then, with the result that
productive effort in agriculture was relatively less remunerative then
than it has been since. The gain of agricultural prices over other prices
reflects the effect of a readjustment made by the effort of people to get
into the line of production that pays best. In other words, the number
of farmers and farm laborers has been increasing relatively less rapidly
during the last twenty-five years than the number of people in other
pursuits. Agricultural products, as a result, have become relatively
scarcer and their prices relatively higher.

It will be noted that at the beginning of the period farm wages were
well below both the general price level and also the price level of agri-
cultural products, but that from 1885 to 1915 their trend was very
close to that of the price of agricultural products.[11] During the war
period, however, and afterward, the prices of agricultural products
rose more rapidly than farm wages, until the break came in 1920, after
which prices of agricultural products declined more sharply than wages.
The significance of these changes in trend is discussed later in the
bulletin.

The low level of farm wages shown for the early part of the period
would have been even more marked if the curve had been extended back
to 1866. The low wages of farm labor between the close of the Civil
War and 1890 is due to a number of causes. During the war, northern
farmers had been able to maintain and even increase the volume of their
production, in the face of a severe labor shortage, by increasing the use

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[11] The higher level of wages shown in the chart from 1892 to 1909 is due to the fact
that between those dates the actual wage figures from which the relative figures used in the
chart are derived, are averages for the growing season and not for the whole year, as is true
of the figures for the other years. They are, therefore, somewhat higher. It is impossible to
get whole-year monthly average figures for this period.

of machinery. With demobilization, the labor market was flooded and the industrial development of the country was not then great enough to absorb the ex-soldiers readily. Many thousands of them took home-steads, but this did not wholly relieve the over-supply, because for lack of funds and other reasons, these claim-holders were not able at once to develop their land into productive farms capable of furnishing full-time employment for the settlers and their families. Further, there was, during this period, a heavy immigration of North Europeans who came to this region to establish farms. Later, when the farms were improved and production on them rose to normal, the wage level began to follow very closely the price level. The farmer can not long pay high wages in the face of falling prices, nor can he long continue to get help at low wages when prices have risen; for high prices prompt increased production both in agriculture and in other lines and conse-quently increase the demand for labor with a resulting rise in wages. The failure of farm wages to fall immediately with the fall in the price of farm products in 1920 will be explained later.

The curve representing horse prices in the chart is based on United States Department of Agriculture estimates of the average value of all horses on the farms of Minnesota. It shows two outstanding variations from the trend of the other price curves of the chart. The first is the extreme decline during the low-price period of the nineties, and the other is the decline during the late war at a time when all other prices were rising rapidly. Horses on Minnesota farms are both a product and a means of production. They are produced mainly for use on the farm, but there is normally in the state a small surplus for sale and the value of all horses tends to be expressed in the prices which can be secured for this small surplus. Further, because horses mature slowly and wear out slowly, the supply does not respond quickly to changes in price. Hence they are subject to rather extreme price fluctuations, but these fluctuations necessarily come at wide intervals.

It was impossible to get annual figures representing the value of farm machinery before 1890. However, the figures shown are sufficient to give us a general idea of the trend of their prices. During the period from 1890 to 1910 the prices of machinery, tho not sagging greatly in the years of lowest prices, in general were declining relatively to the gen-eral price level and to the prices of farm products. This is part of a movement dating back to the introduction of the more modern farm machines and is to be accounted for mainly by the growth in efficiency in manufacture and consequent reduction in the cost of producing the machines. The information we have on machinery prices indicates that they behave quite similarly to the prices of any class of goods which can be freely manufactured in amounts to meet the changing volume of demand. The price of such goods tends in the long run to be governed

by the costs of manufacture, and as these costs necessarily rise and fall with changes in the general price level, the close correspondence between the prices of machinery and those of general commodities, as shown by the chart, is to be expected.

The price of no other factor of agricultural production has increased so rapidly as that of land. Table XII shows that in 1880 farm land in Minnesota averaged $14.45 per acre. There was, apparently, no decrease in the nineties as in the case of labor, horses, and machinery, but the increase after 1900 was much more rapid than previously, and in 1910 the average price per acre was more than three times as high as it was in 1880. Land values during the war period did not rise quite as soon as wages and other prices, but by 1919 they had almost doubled the 1909 rate, and in 1920 they were two and one-third times the 1909 rate. The 1920 census shows the average for the state to be $109.25 per acre.

The reason that land prices rise rapidly is that the supply of land can not readily be increased in response to expanding need for its use in the production of agricultural commodities. Like other means of production, it tends to have its value determined by the value of its products; but unlike livestock and machinery, which can be produced in quantities to keep pace with either an increasing or decreasing demand, and labor which can be moved from one situation to another in response to changing need, land is fixed both in amount and location. Hence, when an expanding wheat market calls for more wheat, the supply of all the things needed to produce it may be pretty readily increased except land. Hence there results a scarcity of wheat land. This scarcity of wheat land causes a scarcity of wheat, which causes the price of wheat to rise. This in turn causes the price of wheat land to rise because people are now willing to pay more than before, either in annual rent or in actual purchase, for the opportunity to raise wheat. If land could be manufactured like grain binders, this scarcity would not appear and the price would not rise appreciably above the cost of producing land. In 1880 there was considerable wheat land still unused, which was capable of as high yields as much of the land then in use. The price of land in Minnesota at that time represented largely improvements and advantage of location. However, as the industrial population increased both in this country and abroad, and more wheat and other products were needed, practically all the usable lands were occupied. Thereafter, as demand for these products still further increased, the series of causes just described was set in motion, with the result that prices of land have risen much more rapidly than those of labor and the other means of production the supply of which could be increased at will.

CHANGES IN AMOUNTS OF OTHER FACTORS USED WITH A GIVEN AMOUNT OF LABOR

We are now ready to note how these varying rates of increase in the prices of the factors of agricultural production are related to the proportions in which they are actually used. When the price of any one factor rises more rapidly than that of the others, does it follow that the farmers must be using less of this more expensive factor and more of the cheaper ones? It has been generally assumed that they are using less of the expensive factors. The census gives us at ten-year intervals information which, combined with other data, enables us to measure with some degree of accuracy proportional relationship between labor, land, machinery, and horses. Table XIII (see also Fig. 7) is designed to show this relationship. Because in this discussion we are interested primarily in labor and wages, the table has been constructed to show for the different years: (1) how many units of the other things have been used for each man in the state engaged in farming—including, as before, both farmers, their mature sons, and their hired men; and (2) the percentage of change in these proportions from those of the base year, 1880.

TABLE XIII

AMOUNT OF LAND, MACHINERY,* AND HORSES USED PER MAN ENGAGED IN AGRICULTURE IN MINNESOTA, 1880–1910

Date	Actual No. of units				Percentage of change			
	Land (acres)		Ma-chinery (value)	Horses (No.)	Land (acres)		Ma-chinery (value)	Horses (No.)
	Total	Im-proved			Total	Im-proved		
1880	109.2	59.1	$106.69	1.7	100.0	100.0	$100.0	100.0
1890	110.7	66.0	100.68	2.3	101.3	111.7	118.2	130.5
1900	111.9	78.6	128.27	2.3	102.5	133.0	177.8	134.5
1910	108.5	77.0	205.19	2.4	99.1	130.3	190.4	137.9

* The figures in the first machinery column were found simply by dividing the total farm investment in implements and machinery as reported by the census, by the number representing the men engaged in agriculture. The figures do not show the actual increase in the use of machinery because the money investment depends not only on the amount of machinery used but on its price. It was necessary, therefore, to derive the percentage of change for machinery by a different method from that used for the items in which we have non-money units. This was done by first getting percentage-of-change figures on machinery investment and dividing these for each year by the percentage-of-change figures on machinery prices as given in Table XII. This gives the percentage-of-change figures used in this table. They are only an approximation to the actual rate of increase in the use of farm machinery in Minnesota agriculture, but it is believed to be a fairly close one.

The table shows several interesting things: (1) That altho the price of land almost trebled between 1880 and 1910 and wages increased only 75 per cent, the rates of labor to land remained about constant. Part of the increase in the value of land is of course, accounted for by the increase in the amount of improved land, which really represents an increase in capital in the form of clearing, draining, fencing, etc.

(2) Altho the price of machinery remained about constant during the period, the amount used per laborer and per acre nearly doubled. (3) While the price of horses was doubling, the number used increased only one third in relation to labor, and decreased one third in relation to machinery.
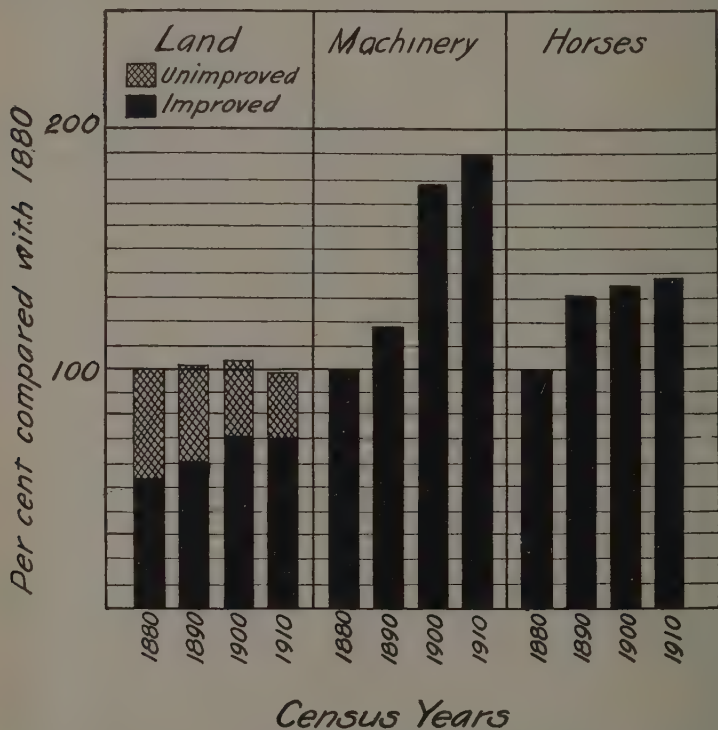
Fig. 7.　Changes in Average Amounts of Land, Machinery, and Horses Used with Each Man Engaged in Agriculture in Minnesota, 1880-1910

Note that the amount of machinery almost doubled and horses increased nearly 40 per cent between 1880 and 1910, while the amount of land has remained almost constant. This means greater intensity of cultivation in terms of power and machinery tho not of labor.

As classified by the census, improved land in Minnesota means in general cropped land, while unimproved land is mostly permanent pasture. Some of the latter is rough, uncleared, or undrained, tho much of it is highly productive as a means of supporting livestock enterprises; but under normal Minnesota conditions, pasture is a much less intensive use of land than cropping. Hence the increase in improved land really represents a greater utilization of land in terms principally of capital.

How the farmer has been able to increase the utilization of his land—that is, farm more intensively—without significantly increasing his labor,

is largely explained by the figures on machinery and horses. The great increase in machinery means not only that the implements used were better and of higher capacity and thus able to do more and better work, but also that more and more farm operations formerly done by hand or by the use of primitive implements were being done by improved, high-capacity machines. This development in farm machinery enabled farmers both to devote more of their land to the more intensive uses and to do much better and more intensive work on their constantly increasing area of cropped land. Along with this, undoubtedly, went a much higher utilization of the farmer's time. He was employed more constantly and his work was much more effective as measured in volume of product. Work animals likewise were used more effectively by increasing the number of days of employment per season. This is evident from the fact that their increase in number was at a much slower rate than that of machinery, notwithstanding the fact that in the early part of the period oxen were of much more importance than in the latter part. The growing importance of livestock enterprises, particularly dairying, which requires considerable labor, could not have accompanied this growing intensity in the use of land without a corresponding increase in the labor supply except for this phenomenal growth in the use of machinery.

We must conclude, therefore, that the Minnesota farmer has found it wise to increase the utilization of his land by using more machinery per acre rather than more labor: (1) because it is cheaper; (2) because it requires less management; and (3) because it is more effective than additional labor in the operations involved in Minnesota farming. It was unnecessary for him to increase his use of horses as rapidly as machinery because new types of machines, new methods of operation, and changes in the type of farming enabled him to utilize his work animals more completely by working them more days of the year.

Some other facts not brought out in Table XIII bear directly on the matter of changing proportions. (1) In spite of the increase in the value of land, each farmer in 1910 was handling 177 acres of land, of which 71 per cent was improved, compared with 145 acres in 1880, of which 54 per cent was improved. (2) In spite of a 75 per cent increase in wages, each farmer was managing, in addition to his own labor, two thirds of a hired man in 1910 as compared with one third of a hired man in 1880. (See Table I.)

Thus in terms of management, each farm operator in 1910 was managing 22 per cent more land than in 1880, and 25 per cent more labor, counting his own. The increase in improved land during this period from 78 to 126 acres per farm represents an increase of 56 per cent in amount of capital managed in the form of land improvements. Further, each farm operator managed 138 per cent more machinery and 74 per

cent more horses. No figures are available to show the relation of managerial incomes to this very great increase in the ratio of land, labor, and capital to management; but it is obvious they bear no regular proportion to each other. The farmer's primary concern is to get the highest total net gain for himself rather than the highest rate of gain on the cost of land or any other factor or even on his total investment. His profits may be considerably larger with a low rate of return on a large investment than with a high rate on a small investment. It is reasonable to assume that as he expands the area of land he uses, thereby increasing his investment in land, in terms either of annual rent or purchase price, the returns on the successive additions to such investments will decrease because the land itself will be less thoroly used as he uses more and more of it. But he will find that his whole net gain is increased by these additions as long as there is any appreciable margin between what the additions cost him and the increase they bring to his total receipts.

As for labor, it is obvious that a farmer should hire no labor on which he can not make at least a little profit. That is, unless the hiring of a man for the whole or a part of the season will result in adding something to his total net gain for the year, there is no object in hiring. This gain may come through saving a part of the crop at harvest which would otherwise have been lost, or it may come through expanding the business by hiring an additional man and renting or buying additional land and equipment. It is undoubtedly true in hiring men in order to expand the business, that, beyond a certain limited number, the additional investment in wages, rent, interest on additional land, and the other expenses going with expansion, bring a lower and lower margin of gain the further the expansion is carried. This is due primarily to the fact that the more men a farmer has, the less carefully he can direct the work of each of them and the greater the loss of time, equipment, and supplies, because the oversight is less thoro. Herein is found the real limit to the number of men a farmer should hire. Hence in most types of farming and under most conditions in all types, the farmer finds that he reaches the limit of profitable hiring very quickly. Indeed, on a great many farms the farmer, taking into consideration the uncertainty of yields and prices, finds it safer to expand his business only to the limit set by the labor of himself and the members of his family, perhaps hiring a little additional labor during the rush periods of the season. Other farmers, usually those having little or no family labor, find it profitable to hire one or two men steadily, while an occasional farmer, who possesses unusual managerial ability, may successfully engage from six to twelve or more men with a correspondingly large amount of equipment, land, and productive livestock.

There are, of course, many conditions which cause changes in the limits of profitable hiring. When the prices of products rise faster than

wages, as they frequently do in periods of business expansion, it will pay the farmer to hire more men, provided he can obtain the additional land and equipment necessary to employ them. On the other hand, a marked fall in the prices usually leaves wages temporarily at a higher level. In such a case, farmers, like all business men, find it necessary to contract their business and hire fewer men. A change in the organization of the farm from a type requiring little labor in proportion to land to one requiring much, or vice versa, necessitates a corresponding change in the amount of hired labor. The shift from grain farming to dairying in parts of this state is resulting apparently in a larger proportional number of year-round hired men. It is to be expected, also, that as experience and education come to play a large part, the managing capacity of farmers will grow. This may be expected to create greater competition for men, with the result that the more skilful managers get the men, while the less skilful tend to drop out of the business.

RELATION OF FARM WAGES TO GENERAL BUSINESS CONDITIONS

We have already noted the extraordinary changes in wages and prices during the last six years. It is worth while to analyze these in their relations to each other. It is generally assumed that these changes were occasioned by the World War and that with a return to "normal" such changes are not to be expected. It seems evident that this series of changes received its impetus from the war and that the changes would not have reached such magnitude but for the profound influence of the war. However, the normal in business is a succession of changes now generally known as the business cycle. Conditions during the last six years have forced public attention to this phenomenon so that the several phases of the cycle and the characteristics of each phase are pretty generally known. The extraordinary extremes of business activity so far as they can be revealed by price changes are well brought out by the index figures of the Bureau of Labor Statistics already presented in this bulletin. How this unusual upheaval has affected the farmer's business, particularly with reference to his ability to hire labor, is discussed in the remaining portion of this bulletin.

NATURE AND CAUSES OF THE FARM LABOR SHORTAGE

One aspect of the business cycle just described is the recent unusual shortage of labor. This shortage began to appear in 1917 and became acute in 1918 as a result of the formation of the national army. It was relieved somewhat in 1919 by the demobilization of the army, but became acute again late in 1919 and the early part of 1920, owing to the

remarkable expansion in industry and trade which reached its climax in that period. This expansion was terminated by the crisis of the summer of 1920, and with the sudden curtailment of industry, the labor shortage was ended and unemployment began to appear in certain industries.

The supply of farm labor was affected much the same as labor in general. The figures in Table XIV, taken from the April numbers of the Monthly Crop Reporter for 1920 and 1921, reflect the view of the situation held by the farming class. They are based on the estimates of farmer correspondents of the Bureau of Crop Estimates in reply to inquiries sent out about March 1, before the opening of the crop season. They indicate that in the collective judgment of the Minnesota correspondents as expressed at the beginning of the 1920 season, there would be 108 farm jobs open in the state for every 100 open in the years, say from 1909 to 1914. At the same time, for every 100 men seeking farm jobs in these earlier years, there would be only 76 in 1920. Taken together, these two conditions would mean that for every 100 farm jobs open in Minnesota in 1920 there would be only 71 men to fill them. However, these correspondents estimated that in the season of 1921 there would be only 92 per cent as many farm jobs open as in the years before the war and 97 per cent as many men seeking farm work. This would mean that for every 100 jobs there would be 105 job seekers.

TABLE XIV

ESTIMATED SUPPLY AND DEMAND OF FARM LABORERS, 1918–1921

	Supply of farm labor (per cent of normal)				Demand for farm labor (per cent of normal)				Ratio of supply to demand (per cent)			
	1921	1920	1919	1918	1921	1920	1919	1918	1921	1920	1919	1918
United States	95.2	72.4	84.4	72.8	87.5	105.3	101.8	101.4	108.8	68.8	82.9	71.9
Minnesota	97.0	77.0	86.0	78.0	92.0	108.0	103.0	100.0	105.0	71.0	83.0	78.0

Probably these figures reflect approximately conditions of supply and of demand for farm labor so far as they can be forecasted at the beginning of the season, but they need careful interpretation in order not to be misleading. In the first place, it is impossible to foresee the conditions which may develop during the season both in agriculture and in general industry. As a matter of fact, in the season of 1920 the growth of unemployment in industry released large numbers of men for farm work, particularly for the harvest season, and the supply of labor was adequate.

In the second place, such figures are likely to be misleading when taken alone because they give no idea of how much a given shortage in hired laborers affects the total supply of farm labor. Specifically,

what effect would it have had on the farmer's business and on the agricultural output of Minnesota if twenty-nine out of every hundred possible farm jobs in the state had remained unfilled in 1920? This depends first on how important a place the hired man holds in Minnesota agriculture, and second, on the extent to which his place may be taken by a larger use of machinery. No figures on the first point are available more recent than those of the 1910 census. At that date, of the 256,544 persons reported as engaged in agriculture in the state, 145,589 were farmers, 61,026 were given as laborers working on the home farm, that is, they were in the family labor class, and 49,928, or 19.4 per cent, were hired help. (See Table I.) There was, therefore, about one hired man for each three farms. A reduction of 29 per cent in this 19.4 per cent of the farm labor supply would really be a reduction of only 5.6 per cent of the total number permanently engaged in agriculture. Probably there was some reduction also in the family labor through farmers' sons leaving the farm in larger numbers than usual, but it is doubtful if both these sources of shortage together amounted to 10 per cent of the whole number of those normally engaged in farming. Even if the shortage had amounted to 10 per cent, it would not have been so serious in view of the possibility of offsetting a lesser use of farm labor with a greater use of farm machinery.

The third and most essential reason why such figures as those of Table XIV can not accurately forecast the labor situation for the season is that they can not, in advance of the hiring season, be based on any actually existing wage level. Demand and supply are always with respect to given prices, and at the time these estimates were reported, no labor prices had been established.

If farmers bid strongly enough for laborers to draw them from other lines of employment, the labor "shortage" in farming disappears. A shortage in an industry such as agriculture really means, therefore, that employers in that industry are unwilling or unable to pay enough wages to get the help needed to develop their business as fully as they would like. It will usually be the less efficient employers who have to go without labor. That such a condition as this existed to a degree in agriculture for several years prior to 1921 is indicated in Table XIV. The 1921 figures in this table show how these conditions have changed since the crisis. The effects of the change on wages will be apparent in the farm wage figures recently reported for the season of 1921.

Two conditions doubtless contributed to the so-called shortage of farm labor. The first of these was the unusual profits in certain manufacturing businesses during the war and just afterward, which have made possible the payment of unusually high wages, thus creating unusual competition for the farmer's labor supply. The second of these was the general scarcity of labor. The hasty mobilization of an army

of more than four million men produced a temporary acute shortage. Casualties and disease permanently removed about 100,000 of these men from the labor supply. This, however, is almost a negligible fraction of our total labor supply. The unsettled condition of the demobilized men, and to some extent of all the laboring population, which came as a result of the war, was probably a more important reason for the shortage. But the most important of all the war's effects on the supply of labor, was its effect on the rate of immigration. Table XV shows the net permanent immigration for the thirteen years ending in 1920. These figures are exclusive of the entrance and departure of transient travelers.

In the ten years between 1900 and 1910 the average annual increase in the number of people gainfully employed in this country was, according to the federal census, 909,103. In 1910, those gainfully employed were 42 per cent of the total population. For the five fiscal years prior to the European war, net immigration averaged 746,369. Assuming that half the immigrants are potential wage earners, this would mean 373,185 wage earners per year. This number is 41 per cent of the average annual increase in the income-earning portion of our population.

TABLE XV

PERMANENT IMMIGRATION TO AND EMIGRATION FROM THE UNITED STATES, 1908–1920*

Year	Immigration	Emigration	Net Immigration
1908	782,870	395,073	387,797
1909	751,786	225,802	525,984
1910	1,041,570	202,436	839,134
1911	878,587	295,666	582,921
1912	838,112	333,262	504,910
1913	1,197,892	308,190	889,702
1914	1,218,480	303,338	915,142
1915	326,700	204,074	122,626
1916	298,826	129,765	169,061
1917	295,403	66,277	229,126
1918	110,618	94,585	16,033
1919	141,132	123,522	17,510
1920	430,001	288,315	141,686

* Annual Reports of the Department of Labor.

In the fiscal year 1915, the first year of the war, net immigration fell to 122,626, thus supplying less than 7 per cent of this normal yearly increase. In the fiscal year 1918, the first year of our participation in the war, net immigration fell to 16,033, furnishing on the basis of our assumption, only 8000 workers, or less than one per cent of the normal annual increase in bread winners. The figures for 1920 indicate that immigration is again settling back to pre-war volume.

There are no adequate grounds on which to base an estimate of the effect of these several sources of loss on labor supply. The nearest approximation which can be made is that between 1914 and 1919 the average additions to the wage-earning population were reduced to probably 60 per cent of normal, while the subtractions, due to death, disease, and other causes, have been slightly above normal. Doubtless as many men were working in 1919 as in 1914; but during this time our industries were expanding rapidly.

The farm labor shortage of 1918 and 1919, however, was due as much to the shifting of men from agriculture to other industries as to the general labor shortage. The other industries were short of labor because of their great expansion. Some of this expansion preceded, but more of it followed our entrance into the war. Ship-building, camp construction, and numerous other lines of activity carried on under government contract, also added greatly to the non-agricultural demand for workers. The relaxation following the armistice set off a period of extravagant spending, which gave a still further boom to manufacturing. We have no statistical measure of the extent to which this heavy demand for manufactured goods during the war and afterward actually drew laborers from agriculture. As the rural birth rate is normally higher than the urban, and as improved methods in agriculture, coupled with the more rapid development of trade and industry, are constantly reducing the ratio of those engaged in agriculture to those otherwise employed, there is normally a constant flow of workers from agriculture to urban pursuits. But there is little doubt that this flow was of greater volume during this period of industrial expansion; and that the back-flow, which is never large, was smaller than ever.

The most important factor in the relative attractiveness of employment in different industries is the wage rate. However, actual wage rates in different occupations are hard to compare. They are reported for different units of time ranging from the hour to the month. In the case of farm labor, board and other benefits are given in addition to the money payment. We also have no statistics on hours and seasons of employment. For all these reasons we must resort to a comparison of the percentage of change in the wage rates for the various industries and ascertain where the rate of increase has been most rapid. Even this does not take account of unemployment. In industry, the part of the entire year for which the laborer is employed is primarily a matter of business conditions, while in agriculture it is mainly a matter of weather and the seasonal nature of the various farm tasks. The laborer's total yearly income may be increased or decreased by changes in business conditions to a much greater degree in industry than in agriculture.

In comparing changes in wages over a period of years in different industries as a means of getting at conditions in these industries, it is important to use as a basis for comparison some year or years in which conditions are as stable as possible, in which the wage rates then existing reflect a relatively settled distribution of labor between the industries. The statistics for the year 1915 indicate that at this period the various industries, including agriculture, were closely in balance with the demand for their products and that the distribution of labor supply between them was reasonably stable. Hence 1915 is made the base year in Table XVI, in which the wages of farm labor are compared with the wages in various industrial occupations in Minnesota during the years 1915 to 1920. (See also Fig. 8.) The farm wage figures are the estimates of the United States Department of Agriculture already referred to (see Table XI), and the other figures are based on the wages of industrial laborers of all grades and classes whose accident compensation cases, to the number of several thousand each year, are passed upon by the State Department of Labor and Industry. The average wages in all non-agricultural industries combined increased in the six years only about half as much as agricultural wages. In certain specific industries, however, such as mining, construction, and metal working, the wage increase has been almost as great as in agriculture. To the
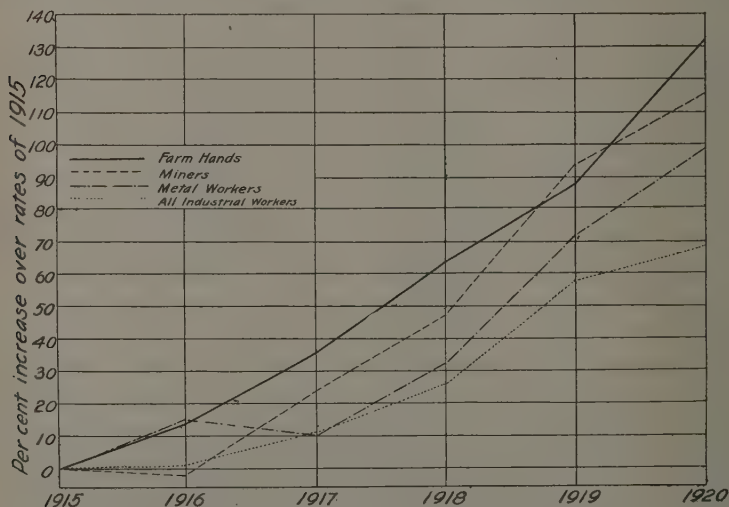
Fig. 8. Comparative Increase in Wage Rates in Minnesota, by Occupations, 1915-1920

Farm wages rose more rapidly for the most part than industrial wages, but the gross income of farm hands probably increased less than that of industrial workers because of the greatly increased working time of the latter.

non-agricultural wages must be added payment for a large amount of
overtime in the period of expansion, and a still larger allowance for
greater regularity of employment. In normal times, unemployment
in many leading industries runs as high as 25 per cent of the working
days of the year. This was reduced almost to nothing during the period
of industrial expansion.
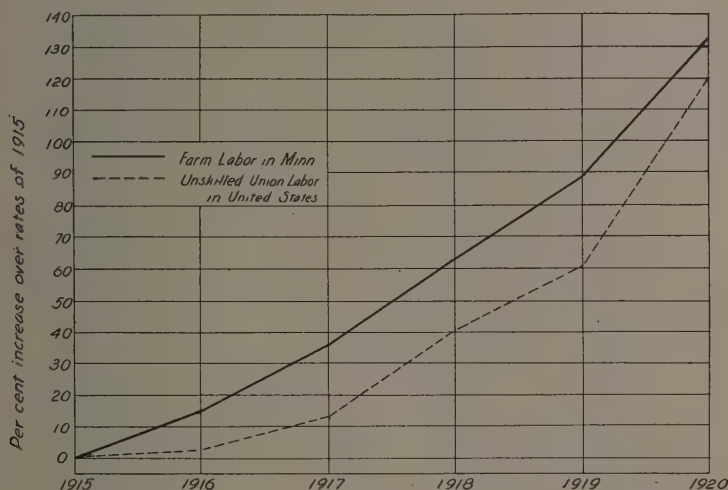
Fig. 9. Increase in Farm Wages in Minnesota Compared with Those of Unskilled Laborers,
Average for the United States, 1915-1920

Farm wages rose more rapidly than the others until 1919. Thereafter industrial wages
rose more rapidly because of greater prosperity in fields other than agriculture. (See Fig. 10.)
Increase in employment time caused the gross income of the union laborers to rise more
rapidly than the curve indicates.

Table XVII gives wage data for the whole United States. It pre-
sents the average of union wage scales in certain occupations for the
United States covering the period from 1915 to 1920 as reported by the
Bureau of Labor Statistics. This table contains wage figures for only
those occupations which require either unskilled or but slightly skilled
laborers, the supply of which can be quickly recruited by drawing men
from other occupations. It will be noted that during the six years in
question the wages in all these lines more than doubled. As a matter
of fact, they increased much more than the wages of the more skilled
workers with whom these men are associated. They did not increase
quite so much as farm wages, in Minnesota. To the wage increases
given, however, must of course be added allowances for overtime and
more regular work. These facts are shown graphically in Figure 9.

TABLE XVI

COMPARISON OF FARM AND OTHER WAGES IN MINNESOTA, 1915–1920

Kind of work and unit	Wage scale						Per cent of 1915 scale					
	1915	1916	1917	1918	1919	1920	1915	1916	1917	1918	1919	1920
General farm work (month)*	$28.80	$33.00	$39.00	$47.10	$53.70	$67.00	100.0	114.6	135.4	163.6	188.0	232.6
Harvest (day)*	2.33	2.55	2.96	3.90	4.30	5.10	100.0	109.4	127.4	167.4	188.0	218.8
Approximate value of board, etc., per month on farm*	13.00	11.70	15.00	15.60	21.30	21.40	100.0	90.0	115.3	120.0	163.8	164.6
Average all non-agricultural												
Industries (week)†	14.95	15.00	16.64	18.74	23.57	25.20	100.0	100.3	111.3	125.4	157.3	168.5
Mining (week)†	16.00	15.80	19.68	23.54	30.61	34.53	100.0	98.8	123.0	147.1	193.3	215.8
Lumbering (week)†	12.30	11.74	13.77	15.78	20.07	21.36	100.0	95.4	112.0	129.0	162.3	173.6
Construction (week)†	17.60	17.89	19.00	21.54	28.08	34.61	100.0	101.7	108.0	122.4	161.1	196.6
Wood working (week)†	13.65	13.56	14.00	16.91	20.18	24.80	100.0	99.3	102.5	123.8	147.8	181.6
Metals (week)†	13.97	16.13	15.43	18.38	23.93	27.58	100.0	115.4	110.4	131.5	171.3	197.4

* From Monthly Crop Reporter, Bureau of Crop Estimates, U. S. Dept. of Agr.
† From biennial reports of Minnesota Department of Labor and Industry.

TABLE XVII

AVERAGE UNION SCALE OF WAGE RATES PER HOUR IN THE UNITED STATES, 1915–1920

Occupation	Average rates per hour (cents)						Percentage, 1915					
	1915	1916	1917	1918	1919	1920	1915	1916	1917	1918	1919	1920
Building laborers	31.2	32.7	36.1	42.3	48.2	69.8	100	104.8	115.7	135.5	154.4	233.7
Hod carriers	36.5	37.3	41.6	48.7	56.9	82.5	100	102.7	114.6	134.1	156.7	227.2
Plasterers' laborers	41.7	42.9	45.8	52.8	60.1	87.1	100	102.8	109.8	126.6	144.1	208.8
Steam fitters' helpers	32.8	33.1	35.3	40.9	49.0	70.9	100	100.9	107.6	124.6	149.3	216.1
Blacksmiths' helpers	33.7	30.3	28.7	49.2	55.0	66.3	100	104.8	117.4	171.4	191.6	231.0
Machinists' helpers	27.4	29.2	32.3	41.1	46.0	57.5	100	105.9	117.8	150.0	167.8	209.8
Average percentage of increase	...	...	...	...	...	...	100	103.8	113.8	140.4	160.7	219.4

In such an analysis, account must be taken of the greater increase in the cost of living in industrial centers as compared with the farm. The normal farm wage contract in most parts of the country includes board, lodging, and frequently washing and mending. A fair comparison of wages, then, even on a percentage of increase basis, is not as between gross money wages, but between the money payment of the farm hand and the net amount the industrial worker has after paying in cash for the things the farm hand receives in kind. The best available statistics indicate that the money cost of living in the city increased somewhat more than 100 per cent between 1915 and 1920. At the same time, farmers' estimates of the cost of boarding hired men, as indicated by the difference between wages with board and without board, reported by the Bureau of Crop Estimates, increased only 65 per cent. Undoubtedly, however, farmers place too low an estimate on the value of these perquisites.

In spite of the greater increase in the cost of living in cities, however, the available data seem to indicate that wages in the industries increased faster than on farms. This conclusion, it must be admitted, makes a large allowance for overtime earnings and decrease in unemployment.

In response to the high wages in the industries, many farm laborers moved to the cities, or entered the industries immediately after demobilization. However, the number thus shifting, tho large enough to aggravate the farm labor shortage, was after all but a small proportion of the whole. The great majority of farm laborers, particularly those hired by the month, are young men reared on farms in the same region where they are working, whose services are not needed on the home farm. Their training and interest unite to keep them in farm work in preference to the unaccustomed and confining work of the shop, the factory, or the mine. Many farm hands have little natural aptitude for skilled shop work. While many industrial jobs are almost wholly mechanical and require little or no previous training, the more highly paid lines of work, and particularly some of the unionized lines, require considerable periods of apprenticeship, and can not be entered on short notice in response to a wage increase. Doubtless the fact that agricultural wages themselves rose rapidly was a primary force in keeping much of the farm labor class in their usual employment.

RELATION OF FARM WAGES TO FARM PROFITS

How have the changes in wages and prices that have accompanied recent phases of the business cycle affected the farmer's profits? How have the other changes affected the farmer's ability to pay wages? To answer these questions we must analyze the farmer's receipts and

expenses, the prices he has received for his products, and the prices
he has paid for machinery, supplies and labor. Figure 10 shows the
relation that the prices of farm products have maintained throughout
the period to the prices of other commodities. The curves are based
on the price index figures of the Bureau of Labor Statistics.[12]   In
these figures the prices for January, 1915, are taken as 100 per cent
and the prices for subsequent months are expressed in percentages of
this base. The comparison is between the average wholesale prices of
agricultural products and the average wholesale prices of all commodities
including agricultural products. From the beginning of 1915, agricul-
tural prices rose more rapidly than the average for all commodities
and maintained a higher level until the middle of 1919. From that
point, the prices of general commodities rose above agricultural prices,
and when the downward turn came in May and June, agricultural prices
dropped more rapidly than general prices. In short, so far as wholesale
prices can reveal it, the sellers of agricultural products had the best of
the market during 1915, 1916, 1917, and 1918, but in the recent price
decline they have suffered far more than the average sellers. It is true
that the prices of some commodities, such as clothing, building materials,
and house furnishings, during the latter part of the period of expansion
rose much higher above agricultural prices than the general average of
prices as indicated in this chart, and suffered much less in the decline;
but on the other hand, the prices of such important commodities as
metals and metal products, including iron and steel, did not rise as high
as agricultural prices, tho in the decline they did not fall so rapidly
nor so far.

Figure 10 also throws some additional light on the shortage of farm
labor in the spring of 1920. During the actual fighting, farm products
were among the most vitally necessary war supplies, while many manu-
factured products were for the time in but little demand. With the
armistice, the anxiety over the food supply was relieved; and with the
public danger averted, the regime of saving was relaxed and a reaction
of extravagant buying ensued which created a strong demand for manu-
factured goods, many of which were luxuries or semi-luxuries. Prices
on bread grains and a few other farm products continued to rise, tho
less rapidly, while livestock prices showed a tendency to decline. In
this situation the farmers in the spring of 1920 found themselves in
competition for labor with industries whose products had risen in price
much more than their own and which could therefore force wages to
a level out of the reach of many of the less efficient farmers. Those
who were able to hire did so at the risk of a price decline which might
wipe out all their profits.

[12] U. S. Dept. of Labor, Bur. of Labor Statistics, Bul. 269, and Monthly Labor Review,
May, 1921.

The data on farmers' receipts and costs are by no means complete. For many items of expense, no price figures are available. There are no adequate figures on the increase of rents paid by tenants. The valuation of the farmer's own labor and that of his family, and of the land and equipment which he owned before the changes came, present added problems. Further, there is no accurate information as to changes in the amounts of the different factors of production used as a result of changes in their costs. Enough statistics are available, however, to indicate quite clearly the general trend of farmers' profits during the period.
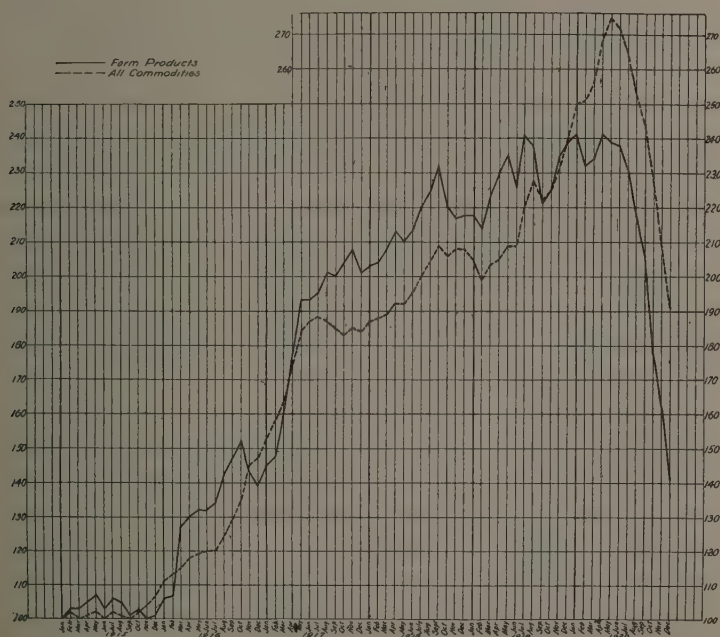
Fig. 10. Wholesale Prices of All Commodities and of Farm Products Compared by Months,
1915-1920

(Bureau of Labor Indexes, prices for January, 1915, taken as base.)
Note that prices of farm products, tho above the level of all commodities from the beginning of 1915 to the end of 1919, did not rise with the latter in 1920, and fell more rapidly when the crisis came.

Table XVIII shows for the United States as a whole the relative rate of change in prices of the things the farmer sells as compared with the prices of things for which he spends his money. (See Fig. 11.) In these figures the prices of each crop and class of livestock are given weight in the averages in proportion to their average importance in the receipts of the farmers of the country for each year. In the same way, the prices of the various articles purchased by the farmer are

given due weight in the average. Things purchased by the farmer include both the things he and his family use directly, as clothing, food, and household furniture, and also the things he buys for use in farming, as feed, seed, fertilizer, machinery, and building material. It will be noted that between 1915 and 1919 the average price of these things increased only 88.7 per cent, and the wages of labor, another important item of expenditure for the farmer, increased only 97.1 per cent, while the price of the two main classes of the things he sells, namely, livestock and crops, advanced 103.7 and 114.6 per cent, respectively. This gain in the prices of farmers' products over the prices of the things for which he spends his money indicates a widened margin of receipts over expenses and consequently larger profits during these five years.

TABLE XVIII

CHANGES IN PRICES OF CERTAIN ITEMS IN FARMERS' RECEIPTS AND EXPENDITURES.
AVERAGE FOR THE UNITED STATES, 1915–1920

Items	Per cent of price in 1915					
	1915	1916	1917	1918	1919	1920
Land, value per acre.......	100	110.8	124.4	135.8	164.2	150.4
Labor, per month..........	100	108.5	135.2	167.6	197.1	228.6
Purchases, price...........	100	111.5	136.5	167.4	188.7	199.1
Livestock, price............	100	117.4	174.1	203.0	203.7	176.0
Crops, price...............	100	131.4	193.3	196.1	214.6	193.1
Crops and livestock, price..	100	120.5	185.2	206.9	212.7	185.3
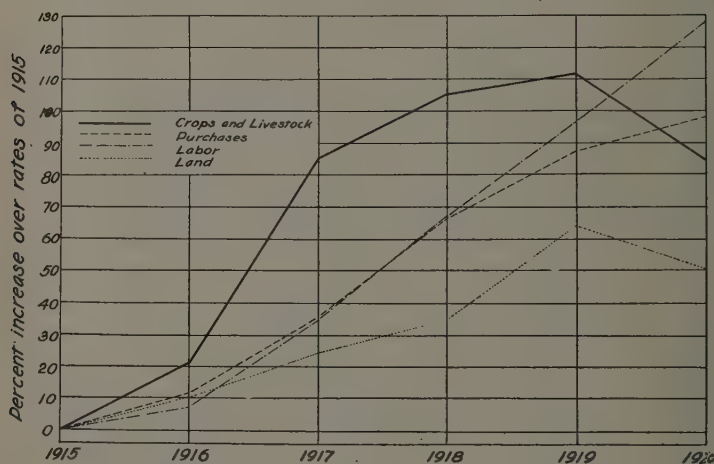
Fig. 11. Prices of Farmers' Products, Purchases, Labor, and Land Compared, United States, 1915-1920

(Bureau of Crop Estimates Prices)

The curves of purchases, labor, and land, which roughly represent farm expenses, in general rose less rapidly up to 1919 than the curve of products, which represents farm receipts. In 1920, conditions were reversed.

To be sure, smaller crops or increased purchases might have kept farm-ers from realizing these higher profits; but statistics show that while in certain years and in certain localities yields have been low for the country as a whole, production increased rather than diminished during the five years in question. On the other hand, the table shows that in 1920 the percentage figures representing the farmer's expenditures had risen very markedly above the figures for 1919, while those representing his receipts had suffered a sharp decline. The figures of this table bear out the general opinion that the farming class for the country as a whole made very substantial profits during the years 1915 to 1919 in spite of rising costs, but that in 1920 they suffered very serious loss.

The Minnesota figures show the same general conditions. Prac-tically complete figures are available of changes in prices of Minnesota farm products during the period. Table XIX gives the figures collected by the Bureau of Crop Estimates, which are "farm" prices in every case. These figures show a range of increase, as indicated in the right side of the table, from 54 per cent in the case of beef cattle, to 292 per cent in the case of potatoes. As potato prices were abnormally low in the base year of 1915, this latter figure has little significance. How-ever, in the three items of most importance in the farmer's income, wheat, dairy products, and hogs, there were increases of 172, 108, and 187 per cent respectively between 1915 and 1919. In general and with the important exception of beef cattle, the increases were most marked in the cash crops and cash livestock products, and, with the exception of hay, least marked in the feed crops. The figures showing the aver-age percentage of increase indicate that during the five years in question prices steadily advanced, so that in 1919 the average prices received by farmers for their products were more than two and a fourth times as high as in 1915, but that in 1920 the price drop was so great as to reduce the average to only 56 per cent above that of the base year.

Prices, however, are only one factor in the farmer's gross returns. We need also to know how much he had to sell. Figures on yields give us this information as to crops, while the number of animals at the beginning of the year is probably the best available indication as to the relative amounts of livestock and their products that may be sold during the year. Table XX gives yields and value per acre of the leading crops in Minnesota from 1915 to 1920 as collected by the Bureau of Crop Estimates, and Table XXI gives the number of the leading classes of livestock reported as being on hand January 1 of the same years.

TABLE XIX

MINNESOTA FARM PRICES OF THE MORE IMPORTANT AGRICULTURAL PRODUCTS, 1915–1920

Commodities	Prices*						Weight†	Percentage of 1915 price					
	1915	1916	1917	1918	1919	1920		1915	1916	1917	1918	1919	1920
Corn per bu............	$0.62	$0.80	$1.10	$1.11	$1.20	$0.51	1.6	100	129	177	179	194	82
Wheat per bu...........	0.92	1.62	2.02	2.04	2.50	1.30	30.0	100	176	220	222	272	141
Oats per bu............	0.32	0.47	0.63	0.63	0.64	0.36	3.6	100	147	197	197	200	112
Barley per bu..........	0.49	0.87	1.11	0.80	1.16	0.62	4.0	100	178	227	163	237	126
Rye per bu.............	0.81	1.27	1.67	1.50	1.30	1.22	..	100	157	206	185	160	150
Flax per bu............	1.76	2.40	2.96	3.41	4.45	1.83	2.5	100	137	173	194	253	104
Potatoes per bu........	0.39	1.30	0.91	0.75	1.53	0.80	..	100	337	233	192	392	205
Hay (tame) per ton.....	6.40	7.00	12.10	14.10	14.50	11.20	15.0	100	109	187	220	227	175
Butter per lb..........	0.26	0.29	0.38	0.40	0.54	0.57	7.0	100	112	146	154	208	219
Eggs per dozen.........	0.16	0.17	0.26	0.30	0.33	0.35	9.0	100	106	163	187	206	225
Beef cattle per cwt....	5.00	5.80	7.30	7.70	7.70	5.00	12.0	100	116	146	154	154	100
Swine per cwt..........	5.60	8.80	16.10	16.10	12.60	9.00	..	100	157	287	287	225	160
Dairy cows per head....	58.10	58.00	68.00	81.10	85.30	90.20	..	100	101	117	139	147	155
Horses per head.......	148.00	145.00	142.00	145.00	133.00	131.00	..	100	98	96	98	90	88
Average per cent.......	...	...	...	...	...	...	...	100	147	201	206	229	156

*The particular prices selected for each product are the ones having most significance for the farmer: the one obtaining when he sells the bulk of his product. The December price was taken for all grains and hay, the December 15 price for beef cattle and swine, the March 15 price for horses and dairy cows, the April 1 price for eggs, and the June average for butter. The figures in this column indicate the varying importance given to the several products in making up the average percentage of increase in prices. Most of the weight for corn and other feed crops is included under the various forms of livestock to which they are fed.

† The weight is given for each product.

Those for which no weight is given were not used in making up the average.

TABLE XX

VALUE AND YIELD PER ACRE OF LEADING CROPS IN MINNESOTA, 1915–1919

Crop	Value per acre (dollars)						Yield per acre (bushels)					
	1915	1916	1917	1918	1919	1920	1915	1916	1917	1918	1919	1920
Wheat	12.31	15.30	35.35	42.64	23.50	12.61	17.0	7.6	17.5	20.9	9.4	9.7
Oats	13.76	12.46	23.31	25.83	17.92	13.50	43.0	26.5	37.0	41.0	28.0	37.5
Barley	14.94	16.53	29.97	24.80	23.20	15.50	30.5	19.0	27.0	31.0	20.0	25.0
Rye	15.80	19.05	30.90	30.00	19.50	20.74	19.5	15.0	18.5	20.0	15.0	17.0
Corn	14.26	26.80	33.00	44.40	48.00	19.12	23.0	33.5	30.0	40.0	40.0	37.5
Flax	18.48	20.40	28.02	35.46	37.82	17.38	10.5	8.5	9.5	10.4	8.5	9.5
Potatoes	41.34	78.00	101.92	78.75	133.11	76.00	106.0	60.0	112.0	105.0	87.0	95.0

TABLE XXI

ESTIMATED NUMBER OF LIVESTOCK ON MINNESOTA FARMS ON JANUARY 1, 1915–1920

Class of stock	1915	1916	1917	1918	1919	1920
Milk cows............	1,186,000	1,240,000	1,302,000	1,328,000	1,368,000	1,395,000
Other cattle...........	1,208,000	1,275,000	1,400,000	1,600,000	1,632,000	1,730,000
Swine	1,716,000	1,716,000	2,075,000	2,400,000	2,784,000	2,951,000
Sheep	564,000	536,000	541,000	568,000	642,000	668,000
Horses	872,000	890,000	925,000	944,000	950,000	940,000

These figures show that wheat yields averaged approximately five bushels below normal for the years 1916, 1919, and 1920, and five bushels above normal for the other three years of the period. For all the other crops listed, the yield was fairly uniform throughout the period and very close to normal. The number of livestock in the various classes is estimated to have increased throughout the entire period. No figures are to be had on the number marketed from Minnesota, but the receipts given in Table XXII for Chicago, East St. Louis, Kansas City, Omaha, Sioux City, St. Joseph, and South St. Paul indicate that the farmers of the country had a steadily increasing volume of livestock to dispose of during the period of generally increasing prices. In 1920, however, the receipts fell off decidedly.

TABLE XXII

RECEIPTS OF LIVESTOCK AT SEVEN LEADING MARKETS

Year	Cattle, including calves	Hogs	Sheep
1915	8,689,736	21,031,405	11,160,246
1916	10,238,629	25,345 802	11,639,022
1917	12,421,101	20,945,301	10,017,353
1918	14,297,855	25,461,514	12,064,416
1919	13,841,651	25,280,245	14,307,503
1920	11,973,681	22,433,301	11,117,479

With practically normal crop yields from a slightly increasing total acreage, and an expanding volume of livestock and livestock products to dispose of, the average gross receipts of Minnesota farmers were greatly increased by the rapidly mounting prices of the period from 1915 to 1919. Particularly for the years 1917, 1918, and 1919, receipts were very high.

The leading three items of expense in farming are, in order of their importance, rent of land, wages of labor, and expense of using machinery. In addition to these, feeds and fertilizer are bought, and other minor supplies. No comprehensive figures are available on the rent of land. The Bureau of Crop Estimates reports annually on the value of land by states. Table XXIII gives the figures for Minnesota for farm lands, including their improvements. If rent and land values always kept together, these figures would indicate that rents rose 90 per cent in the six years in question. In all probability, the increase in rent has been at least as great as that of land value, but we have no assurance of this and therefore are not justified in using the figure as a positive indication of the change in rent in a comparison of farm receipts and expenses.

TABLE XXIII

AVERAGE VALUE PER ACRE OF MINNESOTA FARM LANDS, 1915–1920

	1915	1916	1917	1918	1919	1920
Price	$65	$70	$83	$87	$94	$124
Per cent of 1915 price...	100.0	107.7	121.5	133.8	144.8	190.1

The annual cost of using farm machinery, including repairs, interest on investment, and depreciation, has been placed, as the result of numerous investigations, at 20 per cent of its inventory value. On this basis, changes in the price of representative machines would reflect with sufficient accuracy changes in the cost of using machinery. Table XXIV shows the wholesale Minneapolis price of a selected group of commonly used implements during the last six years. It also shows the sum of these prices and the percentage of change in this sum in each year. The retail prices paid by farmers is commonly about 25 per cent over wholesale prices.

TABLE XXIV

WHOLESALE PRICES OF CERTAIN REPRESENTATIVE FARM IMPLEMENTS, AND PERCENTAGE OF CHANGE IN TOTAL PRICE, 1915–1920

Implements	1915	1916	1917	1918	1919	1920
Binder, 7 ft. cut........	$117.50	$118.50	$153.45	$198.50	$198.50	$187.50
Mower, 5 ft. cut.........	38.00	38.00	49.45	66.00	66.00	63.50
Gang plow, 14-inch.......	55.50	61.60	75.90	111.00	111.50	111.00
Cultivator, 2-horse rider..	24.75	26.40	34.20	51.00	51.25	51.00
Harrow, 20 ft............	25.00	27.50	26.40	38.00	43.50	40.00
Drill, 10 ft..............	92.00	93.45	112.20	152.00	152.75	152.75
Wagon, 3¼ x 10.........	73.50	77.15	86.90	123.75	138.50	138.50
Collective price......	426.25	442.60	538.50	740.25	762.00	744.25
Per cent of 1915 price	100	104	126	174	179	177

Taking the percentage of increase in the prices of machinery as given in Table XXIV and the percentage of increase in wages as given in Table XVI and combining them into a weighted average series, we have what may be taken as a rough approximation to the rate of increase of the farm expenses during the period.

TABLE XXV

AVERAGE PERCENTAGE OF INCREASE IN MINNESOTA FARM EXPENSE AS BASED ON LABOR AND
MACHINERY COSTS, 1915–1920

	Weights	Percentage increase from rate of 1915					
		1915	1916	1917	1918	1919	1920
Labor ....~	2	100	115	135	164	188	232
Machinery	1	100	104	126	174	179	177
Average	3	100	111	132	167	185	214
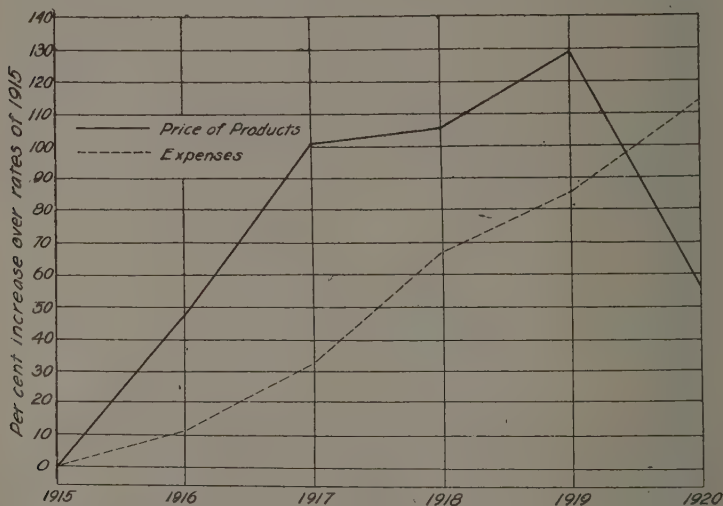
Fig. 12.　Prices of Minnesota Farmers' Products Compared with Their Expenses, 1915-1920

These averages and those of Table XIX, representing changes in
the prices of farm products, are brought together and presented graph-
ically in Figure 12. It is to be kept in mind in interpreting this figure,
(1) that the curves represent merely prices and not total receipts and
total expenditures, and (2) that they represent percentage of change
in these prices from those of 1915 rather than actual price figures. As-
suming that in 1915 the average farmer was getting a margin of profit
sufficient to keep him in the business, this margin on the same volume
of production was greatly increased in 1916 and still more increased
in 1917. That is, during 1916 and 1917 the prices of products were
increasing much more rapidly than the expense. With normal yields
the farmer's profits under these conditions would be growing larger
and larger. In 1918 and 1919, expenses were increasing more rapidly
than the prices of products, but did not increase rapidly enough to
catch up; that is, prices of products were still much higher in proportion

to expenses than they were in 1915, and assuming normal yields, profits were still large in those years. But in 1920, with expenses still rising and prices falling so disastrously, losses were very heavy. Doubtless many farmers reduced their expenditures to some extent in 1920, so that their losses were not so serious as the price and cost lines in Figure 12 would indicate. Many refused to pay the high wages asked in the spring of 1920. Others dismissed their laborers or succeeded in reducing their wages when prices began to fall. There is little evidence that the farmers as a class understood the nature of the business cycle and foresaw the great fall of prices. They did, however, realize that with wages at such a high level, and crop failures always threatening, they were in great danger of coming out with a loss.

The effect on the farmer's profits of the tremendous price changes of the last six years raises the question of the degree to which he is able to take advantage of rising prices through an expansion of his business, and to protect himself from loss by contraction when a price decline is impending. The most outstanding obstacle to both expansion and contraction is the difficulty—in a well-settled mature agricultural community—of increasing or decreasing the land area of the farm on short notice. It is possible to hire additional labor and then to dismiss it, or to buy additional equipment and supplies when conditions make expansion profitable, but usually all the good farming land is occupied and if the area devoted to one crop is increased, it is at the expense of some other crop. Therefore, expansion in the farm business under the stimulus of rising prices must normally take the direction of greater intensity in the cultivation of land either by shifting to more intensive crops or putting more expenditure on the limited areas of the old crops. This means that the farmer may encounter diminishing returns not only from management but from the land. Figures previously quoted (see Table XIV) indicate that farmers during the time of rapidly rising prices were seeking to extend their use of labor, and it is common knowledge that they bought more equipment in the form of larger implements and tractors. It is equally evident from the figures referred to that they are now hiring less labor and doubtless many of them would like to dispose of a part of their equipment if they could do it without too great sacrifice. It seems evident, then, that the farmer does expand and contract his business in response to price and cost changes, altho the nature of his business probably sets somewhat closer limits on this adjustment than is true in most lines of merchandising and manufacture. It is quite obvious, also, that these limitations affect his bidding for labor by making the farm demand for labor increase much less in a period of prosperity than the demand from other industries.

The University of Minnesota
Agricultural Experiment Station

Bacteriology and Pathology of
Sterility in Cattle

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BACTERIOLOGY AND PATHOLOGY OF STERILITY IN CATTLE

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INTRODUCTION

Sterility may be defined as the inability to produce young. (1) It may occur in either sex, but the most disastrous effects are produced when the female is no longer capable of reproducing her kind.

IMPORTANCE OF STERILITY TO AGRICULTURE

The question of continued propagation of the species in man is a sociologic one, while in the domesticated animals the economic considerations far exceed others in importance. Agriculture is a basic industry and animal husbandry bears to agriculture an inseparable relationship. The human race is concerned especially in the production of beef and milk and since the toll from sterility is greatest in cattle the economic factor of the disease must be of universal interest.

The development of a race or family of cattle is often dependent upon the successful rearing of calves from the very cows temporarily or permanently rendered sterile. The valuable purebred animal's worth is intimately related to her ability to produce calves of equally high value. When no longer capable of reproduction, her breeding can not be a source of revenue and she must be sold for beef. In the grade herd the importance of the disease to the owner lies in loss of milk production, when he must dispose of a high-producing cow for beef prices. A cow may be regarded as a machine, and must produce from the fuel (feed) she consumes, salable goods in the form of milk and calves. If this is no longer possible her value is small, depending upon market quotations.

In the male the loss from sterility is comparable, but occurs less frequently and therefore is of less concern.

We may thus sum up: Sterility is one of the most serious diseases of cattle. It strikes at the very heart of the animal industry, at times causing losses which are irreparable.

HISTORICAL RESUME

Sterility is not new, for mention has been made of it in veterinary and medical literature since the very beginnings of these branches of science. Until the brilliant research work of Lister and Pasteur led

the way to the modern and rational conception of disease, no advances were made in solving the problem. It must be admitted that altho bacteriology, pathology, and surgery have contributed much to our present knowledge, the physiologist has also added knowledge which is invaluable in dealing with the problems of sterility.

Toward the end of the nineteenth century the interest of scientific men was attracted to the field of comparative veterinary pathology and bacteriology, and much study was devoted to the diseases of the genital tract of animals. At this period the incidence of the disease seems to have increased, probably because of changed conditions in the development of our civilization, and the increased production of livestock. Infectious abortion in cattle also became more widespread and coincident with it, sterility in cattle increased. The inference is not to be drawn that infectious abortion sprang up suddenly, but rather that its importance increased because of the advances in the production of livestock. It is true also that it appeared to be more prevalent because of better recognition by an increased number of scientific observers. It is not the purpose of this thesis to discuss infectious abortion of cattle. This subject, since the time of Bang (1897) (2), has received the attention of scores of competent workers (3). The fundamental facts of infectious abortion are well described, but as infectious abortion is closely related to the increased prevalence of sterility, a passing mention should be made.

The fact that animals may be barren is stated in Genesis, Chapter 31, verse 38. In 1807 "Complete Farmer" mentions abortion as being contagious and as so regarded by farmers (4). In 1885 Nocard's investigations (5) quite clearly set forth the contagious nature of the disease, altho he did not recognize the specific infection. Woodhead, Aitken, M'Fadyean, and Campbell in 1889 (6) showed that abortion could be produced in cows by inserting into the vagina plugs of wool contaminated by the discharge of aborting cows. Until 1897, however, the etiology still remained in doubt. Through the remarkable work of Bang (2), in Denmark, the specific etiological agent was described. This is regarded without serious question as the cause of the clinical entity. "infectious abortion." The work of Bang was confirmed in England in the "Report of the Departmental Committee to Inquire into Epizoötic Abortion" (1909) (7). In America the disease was first definitely established by the identification of the organism *B. abortus* (Bang) by MacNeal and Kerr in 1910 (8). Other early workers who deserve mention for their contributions to the knowledge of infectious abortion are: Zandel, Styrl, Franck, Roloff, Brawer, and Johne. Altho not meeting with ultimate success, their studies did much in keeping the subject alive and open to further research.

In the writings of veterinary obstetritians we find the first mention of diseases leading to sterility in animals. The first veterinary work on this topic appeared in Belgium by Eberhard and Günther, 1793 (9). This was followed by the text of Skellet (10) which made its appearance in England in 1807. From this period on, publications appeared in practically every country, but for the English speaking people no real information was collected into a text until Fleming (11), in 1877, wrote his "Text Book of Veterinary Obstetrics." Hill (1882) (12), in his text, "Bovine Medicine and Surgery," devotes a short chapter to sterility in the male and female. The noted veterinarian, Dieckerhoff, in his "Lehrbuch der Speciellen Pathologie und Therapie für Thierarzte" (1888), gives excellent pathological descriptions (13) of diseases involving the genitalia of the cow. For instance, he classified metritis as acute, peracute, septic, and chronic catarrhal endometritis. Cook (14) and Awde (15) reported independently, cases of bovine endometritis in 1891. In the short paper by Awde we read, "Although I have been in practice for 15 years (1876) I can not recollect that I ever saw a case of this kind prior to the first one here recorded (1889)."

The real beginning of our knowledge concerning diseases of the genitalia of the cow dates from the time of Bang, followed by such contributors as Wall, Holth, Nielson-Sorring, Albrechtsen, Hess, Tuff, M'Fadyean, Zwick, Jensen, MacNeal, Theobald Smith, Schroeder, and Williams. Many others could be mentioned but these were pioneers in their respective countries.

To summarize: The modern conception of sterility has developed during the last twenty-five years, through advances in physiology, bacteriology, pathology, and therapeutics. The fundamental sciences have placed the veterinary gynecologist in a position to cope more successfully with the diseases of the genitalia.

DEVELOPMENT OF THE GENITAL TRACT OF THE COW

Before describing the results of the present investigation, a review of the development of the organs of the genital tract will be given. This, together with their anatomy and physiology, to be described later, is necessary for a clear understanding of pathologic changes that may occur and lead to sterility.

DEVELOPMENT OF THE UTERINE TUBES, UTERUS, AND VAGINA

Early in embryonic life, before the genital ridges have become well marked (about the second month), the ducts of Müller (Müllerian ducts or tubes) develop as two ridges near the peritoneum, near to but independent of the Wolffian ducts. They appear at first as solid rods, and later develop into definite tubes, ending blindly for a time,

then opening into the cloaca. When "hollowed out" each tube opens
into the peritoneal cavity at the future fimbria of the uterine tube.
Fusion later takes place caudally for a variable distance toward the
anterior, thus forming a single tube of the fused portion. The latter
is to become the vagina, vestibulum, *cervix uteri,* and *corpus uteri.*
The anterior ends become the uterine tubes and the middle portion the
cornua uteri. A good description of the development as occurring in
the bovine species is given by Wall (16) as follows:

"The uterus, uterine tubes, and vagina are developed from a double
mesodermal tube, the Müllerian tubes. These tubes merge caudally,
forming the *corpus* and *cervix uteri,* and the vagina. During the fetal
period the vagina opens first into the cloaca (formed by the entoderm),
and then into the *sinus urogenitalis* (formed by the division of the
cloaca membrane), then adjoins the ectoderm. The epithelium of
all three layers of the blastoderm, the simple columnar epithelium of
the entoderm and mesoderm, and the early stratified epithelium (strati-
fied pavement epithelium) of the ectoderm then meet in the *sinus
urogenitalis* (the future vestibulum). Early, even in the third month
in the embryo of cattle (two investigations of embryos of 9.5 cm.),
the stratified epithelium of the ectoderm seems, however, to cover the
wall of the vestibulum (and of the urethra). The simple columnar
epithelium of the mesoderm, bordering on the pavement epithelium
of the ectoderm, which at the limit is at first double, then stratified,
with a rather sharp limit, which is visible first after great microscopic
enlargement. This continues until the fifth month (three examina-
tions of embryos of respectively 18, 24, and 27 cm.), after which a
slow inward growing of the ectoderm epithelium into the vagina is
observed replacing it. A transformation of the mesoderm epithelium
into the stratified epithelium seems not to be going on. The micro-
scopic examinations evidently favor the hypothesis of an inward growth,
as the stratified epithelium often has a staining reaction, differing from
the mesoderm epithelium, but agreeing with the ectoderm epithelium
(especially visible with the Unna-Pappenheim method), and further,
as in the first place the connection by itself, and in the second the
gradual transition from a highly stratified epithelium to a double epi-
thelium indicate a derivation from the ectoderm epithelium. This
"ectodermoisering" proceeds at different rates of speed in different
individuals (five examinations of embryos of respectively 4, 4½, 4½, 8,
and 9 months old). In new-born and other animals (ten examina-
tions; two new-born calves, two calves about 2 months old; two
heifers about 2 years old, and four older cows) the limit of the ectoderm
epithelium was, as a rule, observed at the *os uteri externum,* or in young
animals one to several centimeters behind this; but of the four older

cows the stratified epithelium in two cases was observed in the cervix and in one of these cases up to 4 cm. in front of the *os uteri externum.* It seems, therefore, as if with years the stratified epithelium spreads somewhat at the expense of the columnar epithelium, a fact which is, according to Sobotta (17), already known concerning woman. Several accouchements are considered to favor this phenomenon, which is clearly a consequence of a greater regenerative capacity of the stratified epithelium.

"In the uterine mesenchyme the differentiation between mucosa and muscular coat first makes its appearance at the end of the fourth month and the primitive carunculae begin to be visible at the same time as swelling of the mucous membrane. In the ninth month the uterine glands are first observed, first as solid then as tubular epithelium formations, growing into the mucous membrane, and the new-born calf shows a distinct layer of glands along the entire uterus, except in the carunculae."

DEVELOPMENT OF THE OVARY

At a very early stage of the mesonephros, a narrow strip of mesothelium extending along the medial surface of this structure becomes thicker and the cells become arranged in several layers. These cells become differentiated into two kinds: (1) Small cuboidal cells, with cytoplasm staining rather intensely, and (2) larger spherical cells with clearer cytoplasm and larger vesicular nuclei. The latter are the sex cells, and the whole epithelial (mesothelial) band is known as the germinal epithelium. The sex cells are destined to give rise to the sexual elements—in the female to the ova, in the male to the spermatozoa. This differentiation can not be made at first, but appears at a later period.

The cells of the germinal epithelium increase in number by mitotic division and for some time, at least, the sex cells continue to increase in number by differentiation from the small cuboidal (indifferent) cells, as indicated by the presence of intermediate stages between the two types. Their germinal epithelium soon becomes separated into two layers, (a) a superficial layer which retains its epithelial character and contains sex cells, and (b) a deeper layer composed of smaller cells which resemble those of the mesenchyme, and which give rise to a part, at least, of the stroma of the sex glands. The elevation formed by these two layers projects into the body cavity from the medial side of the mesonephros and constitutes the genital ridge. From the superficial epithelial layer, columns or cords of cells containing some of the sex cells, grow into the underlying tissue. About the end of the first month of pregnancy changes begin in the genital ridge, which differ according to whether ovaries or testicles are to be formed. The ovarian characters are: (1) The surface epithelium does not become flattened;

(2) a layer of surface epithelium, corresponding to the *tunica albuginea* of the testicle, grows between the epithelium and the deeper parts. This layer, however, is of a looser nature; (3) there is a sharp line of demarcation between the cell columns and the stroma; (4) the sex cells continue to increase in size and become more conspicuous.

During the processes of development, the anlage of the genital gland become more or less separated from the mesonephros and finally is attached only by a thin sheet of tissue—the mesovarium. At the same time it begins to grow more rapidly in thickness, becoming oval in shape.

The loose connective tissue spoken of above as corresponding to the *tunica albuginea* of the testicle, grows in between the surface epithelium and the cell columns (sex cords) and effects a more or less complete separation. The sex cords are thus pushed farther from the surface and become marked off from the surrounding stroma and constitute the so-called medullary cords. The cortex of the ovary at this stage is represented only by the surface epithelium, which is composed of several layers of cells and contains numerous sex cells in various stages of differentiation. The ovary may thus be said to be composed of two parts: (1) the *rete anlage* and (2) the *stratum germinativum*. The latter is subdivided into (a) medulla and (b) cortex.

1. The RETE CORDS develop into a group of anastomosing trabeculae which constitutes the *rete ovarii*, situated in the hilum but nearer the cephalic end of the gland. These are the homologues of the *rete testis*. The cells composing them are smaller and darker than those of the medullary cords. In some of the cords lumina appear and are lined with irregular epithelium. This stage represents the height of their development in the ovary and from this time on they atrophy, and gradually disappear.

2. (a) The MEDULLARY CORDS are composed of small epithelial cells and a large number of sex cells. These are surrounded by a stroma. During fetal life they give rise to primary avorian follicles, later they degenerate and finally disappear.

(b) The CORTEX of the ovary at first consists of several layers of small, darkly staining cells, among which are many large, clearer, sex cells, or primitive ova. From the epithelium, masses or cords of cells grow into the underlying tissue, carrying with them some of the primitive ova. These masses are known as Pflüger's egg cords. The epithelial cells give rise to the follicular cells and are seen constantly undergoing mitotic division. The primitive ova increase in size and their nuclei show a chromatic network.

The egg cords break up and become separated from the surface epithelium, so that a single ovum is surrounded by a single layer of epithelial cells. These constitute the primary Graafian follicles. The formation of egg cords is usually completed at birth but in rare instances continues for a short time after birth. The stroma increases so that the egg cords become separated by a considerable amount of connective tissue. Their germinal epithelium becomes reduced to a single layer of epithelial cells.

Each primary ovarian follicle, containing a primitive ovum, is composed of a single layer of flat or cuboidal cells, plus a layer of stroma, which gives rise to the *theca folliculi*. After the follicular epithelium has become several layers thick, a fluid substance known as the *liquor folliculi,* and probably derived from these cells, is secreted around the cells. As the follicle enlarges these pools coalesce and form a single large pool, lying in the center of the follicle. Thus the epithelial cells are crowded toward the outside, where they form a layer several cells in thickness, known as the *stratum granulosum*. The ovum is likewise crowded toward the periphery of the follicle. The little elevation of the *stratum granulosum* in which the ovum is imbedded is known as the *cumulus oöphorus*. As the follicles approach maturity they gradually enlarge, pushing through the cortex until the *tunica albuginea* is reached. Various views are held in regard to the size that the follicle may acquire. In woman the size averages 5 mm., but varies (18). In the cow, Albrechtsen (19) states that "A follicle is regarded as mature when it reaches a diameter of 10-15 mm." According to Hess (20), 10-14 mm.

It must be borne in mind that development of the follicles is slow and they do not reach maturity until the age of puberty. In heifers this may be the 5th, 6th, 7th, or 9th month, but according to Fleming (21) the age of puberty is from 12 to 18 months. Saint Cyr (21) gives the age of puberty in the bovine species at from 12 to 14 months. De Bruin (22) states that on the average the cow reaches puberty at 10 months of age. When the follicle reaches maturity, other conditions being favorable, it ruptures at the surface of the ovary and the ovum is set free. It has been estimated that from 10,000 to 36,000 primitive ova appear in each human ovary, a vast number of which, it may be seen, never reach maturity. The number of ova in the ovary of the cow at birth varies considerably. Heitz (23) estimated the number to be 3800, while according to Käpelli's (24) investigations the number varies within wide limits (6740 to 297,668).

ANATOMY OF THE GENITAL TRACT OF THE COW

1. BONES OF THE PELVIS

The PELVIC GIRDLE (*Cingulum extremitas pelvinae*) consists of the *ossa coxarum*, which unite ventrally in the symphysis pelvis and articulate with the sacrum dorsally.

The *os coxae* is the largest of the flat bones. It is made up of three parts, the ileum, the ischium, and the pubis, which meet to form the acetabulum, a large cotyloid cavity for articulation with the head of the femur. These parts are fused at about 1 year of age.

The pelvic inlet is elliptical and oblique. In a cow of medium size the conjugate diameter is 23 to 24 cm. and the transverse diameter about 18 cm.

The LIGAMENTS of the pelvic girdle constitute important structures in the support of the generative organs. These are (1) dorsal sacro-iliac ligament, a strong band which is attached to the *tuber sacrale* and the summits of the sacral spines; (2) the lateral sacro-iliac ligament, a triangular thick sheet which is attached in front to the *tuber sacrale* and adjacent part of the median border of the ilium, above the great sciatic notch, and below to the lateral border of the sacrum; (3) the sacro-sciatic ligament, an extensive quadrilateral sheet which completes the lateral pelvic wall. Its dorsal border is attached to the border of the sacrum and the transverse processes of the first and second coccygeal vertebrae. Its ventral border is attached to the superior ischiatic spine and *tuber ischii*. Between these it bridges over the lateral border of the ischium and completes the lesser sciatic foramen. The anterior border is concave and completes the greater sciatic foramen.

2. VAGINA

The VAGINA is the passage which extends nearly horizontally through the pelvic cavity from the neck of the uterus to the vulva. In the non-pregnant animal its length is 20-25 cm. In pregnancy its length increases to 30 cm. or more. The retro-peritoneal pouch of peritoneum extends backward about 12 cm. on the dorsal surface; ventrally the serous coat extends backward but 5 cm. In the ventral wall of the vagina, between the muscular and mucous coats there are commonly two remnants of the Wolffian duct, the canals of Gärtner. When well developed (or occasionally cystic) they may attain a diameter of 3 mm., and may be traced forward to the anterior portion of the vagina or even farther along the broad ligaments toward the ovary. They have an opening posteriorly toward the external urethral orifice. Röder states, according to Sisson (25), that the right canal was absent in 52 per cent of cases, the left in only 22 per cent.

The VULVA has thick, wrinkled labia, and both commissures are acute; the ventral one is pointed, and has on it a number of long hairs. It lies about 5 cm. behind and about the same distance below the ischial arch. The external urethral orifice is 10 to 12 cm. from the ventral commissure. Beneath the opening there is a blind pouch, the sub-urethral diverticulum, which is about 3 cm. long and into which the finger may be easily inserted. The two *glandulae vestibulares majores* (glands of Bartholin), are situated in the lateral walls of the vulva, under the *constrictor vulvae*. They are about 3 cm. long and about 1.5 cm. wide. Each has two or three ducts opening into a small pouch of the mucous membrane. This opens just above the floor of the vulva about 3 to 4 cm. lateral to and behind the external urethral orifice. The gland is lobulated, being separated into lobules by connective tissue and muscular bands. The *glandulae vestibulares minores* occur along the median ventral groove. Numerous lymph nodes are present in the mucosa and may be large enough to cause slight prominences. The clitoris has a very short crura, but the body is 10-12 cm. long and is flexuous. Only the pointed end of the gland can be seen in the ventral commissure of the vulva.

The wall of the vagina is composed from within outward of a mucous membrane, a muscular and a fibrous coat. The epithelium is stratified ectodermal epithelium, which in older animals always extends forward, covering the *os uteri externum,* where transition occurs to the columnar epithelium as seen in the uterus. The mucous membrane has no mucus glands, the mucus seen on it supposedly being derived from the cervix and uterus. The muscular coat is composed of fibers having a longitudinal direction. The muscle is unstriped. The fibrous coat is dense and thick and is composed in part of areolar tissue. The peritoneum is reflected over it in places, forming a serous coat.

The vagina is richly supplied with blood vessels and nerves. The arteries are derived from the branches of the internal iliac, viz.: the vaginal, internal pudic, and uterine. The veins correspond. There is a close network of lymphatics throughout the mucous membrane, these draining toward the internal iliac nodes. The nerves are derived from the sympathetic, through the pelvic plexus.

3. UTERUS

The UTERUS lies almost entirely within the abdominal cavity in the adult. It is a uterus bicornis, the body being relatively short. The cornua are relatively long. As a rule the body is less than 4 cm. in length but may occasionally be longer. The muscular and fibrous coats of the inner portions of the cornua walls are connected for a considerable distance anterior to the body, and are invested by a single peritoneal

investment. For this reason, upon external examination the cornua appears to be 15-18 cm. in length, while in reality the length is 35 cm. Their breadth at the body is about 3 cm. The cornua taper gradually toward the uterine tubes where the size is gradually carried out without an abrupt transition from uterus to tube. The free part of the horn curves at first forward, upward, and outward, and then turns backward and downward, forming a spiral coil. In the non-gravid organ the mucous surfaces of the uterine walls are normally in contact with each other. Posteriorly the cavity of the uterus is continuous with the vagina, through the cervical canal.

The CERVICAL CANAL (*canalis cervicis*) is a tortuous canal about 7 cm. or more in length. According to Sisson (25) the length is 10 cm. It can easily be seen that it is dependent for its length upon the length of the *cervix uteri*.

The CERVIX UTERI consists of a constricted portion of the uterus, the circular muscle fibers being more numerous than in the uterus. The walls are very dense (muscular and fibrous), and measure about 3 cm. in thickness. The lumen (cervical canal) in the bovine species is spiral-shaped. It is difficult to dilate. The walls on either side are in quite close apposition except in estrum and during and following parturition. Posteriorly a portion of the cervix projects into the vagina for a distance of 3-5 cm. in the form of a truncated cone the diameter of which varies greatly, but according to Williams (26) approximates its longitudinal dimensions. The projection into the vagina is properly called *portio vaginalis uteri*, or *os uteri externum*. The tip presents posteriorly many longitudinal converging folds in its mucous membrane which remind one of a radiating flower. The cervix anteriorly joins the *corpus uteri* and is called at that point the *os uteri internum*.

Microscopically the uterine wall is seen to be made up of three coats: (1) mucosa (the endometrium), (2) muscularis (the myometrium), and (3) serosa (the perimetrium). There is no sub-mucosa. In thickness the mucosa ranges from 1.5 to 4 mm. The surface is lined by high columnar epithelium which in the cornua is 30-50 microns in thickness, and in the body about 20 microns. The mucosa of the bovine uterus is especially elaborated in parts for the accomodation of the fetus. To these parts the name carunculae, or maternal cotyledons, is applied. It is this specialized formation, especially in the bovine uterus, which forms the maternal placenta of pregnancy and in which connections between the fetus and mother develop. Thus we may divide the mucosa into two parts: (1) The carunculae, (2) the gland mucosa.

1. CARUNCULAE are oval prominences, about 100 in number, either irregularly scattered over the surface or arranged in rows. They are

covered by the ordinary uterine columnar epithelium, and in the virgin uterus form little swellings over the surface of the mucosa. They are 3 cm. in diameter and 1.5 in depth. Beneath the epthelium are found no glands, but numerous connective tissue cells (old and young), fibers, and a few scattered lymphocytes throughout the connective tissue reticulum. Numerous large and small vessels are also noted not a great distance from the epithelial surface. The carunculae do not reach the muscular coat, but only approximate it. There are usually in the area above the muscular coat a few uterine glands which open at the sides of the carunculae, never on their surface. In pregnancy the carunculae undergo a remarkable evolution, seemingly an embryological development, similar to that seen in the uterine glands. Wall (27) considers them as depots of embryonal tissues of great vegetative power. He states that they appear as epithelium and connective tissue with vessels, which develop in pregnancy and undergo involution after parturition. "In pregnancy these carunculae attain the weight of 200 gr., with dimensions up to 9 cm. (length) by 7 cm. (breadth), by 6 cm (thickness), with a stem about 6 cm. long and 3 cm. broad, growing thinner at the caruncula." They present a convex inner surface and are on stalks instead of being sessile. The carunculae in the pregnant uterus show per square cm. from 10 to 30 crypts, often 10 cm. deep, resembling in form a three-, four-, or five-edged, obtuse pyramid, narrowing irregularly toward the peritoneum (outside). Inward (nearest the embryo) they are 0.3 mm., but at the bottom only about 0.1 mm. in width (27). The surface has a deep sponge appearance due to this development. The walls of the crypts are composed of closely arranged fibers and rather numerous fibroblasts, and a few scattered lymphocytes and polymorphonuclear leukocytes. The epithelium of the crypts is simple, low cuboidal, with rather numerous emigrating leukocytes. At the bottom there is a dense, highly vascular, connective tissue. Into the carunculae crypts the chorionic villi of pregnancy grow, one growing into each crypt and branching like a tree to fill the various niches.

After pregnancy has ended the carunculae undergo involution, corresponding to the involution of the entire organ. The reduction in size is rapid, so much so that within three days after parturition they are only one-fifth the volume of those of the last month of pregnancy. Hemorrhages and hyaline degeneration can be observed in the carunculae stromata, together with necrobiosis of the cells (27). The necrobiosis begins at the lumen of the uterus and goes outward (toward the peritoneum). Occasionally blood vessels may show white thrombi. In the crypts the pavement epithelium shows defects. Cells are observed among which are red blood corpuscles, lymphocytes, polymorphonuclear

leukocytes, and remains of chorionic villi which show a granular degeneration. The next step in the involution begins about the fifth day after parturition and ends between the tenth and fourteenth days, during which time the dropping off of the carunculae occurs, as described by Hilty and Sommer (28). It may thus be seen that the loss of the carunculae with considerable mucous membrane, corresponds to the sloughing of the decidua in deciduate animals (as in the primates). The whole caruncula rarely sloughs off, and when it does, only in small portions. The necrotic material passses away in the lochial fluid. After the birth of one calf the carunculae remain larger than in the virgin uterus, reducing in volume to 10 mm. in length (diameter) and 4 to 5 mm. in thickness. They are often slightly depressed at the center. They show in this state a loosely reticular connective tissue, supporting the normal high uterine epithelium of columnar type, through which may be seen fibroblasts, solitary lymphocytes, and in its deeper portion, many large vessels. These have thick walls and fine lumina, some showing hyaline degeneration of the intima and thickened media.

2. The GLAND MUCOSA has as its principal difference from the carunculae the presence of numerous uterine glands. It consists of two layers, (a) an inner layer, called by Ellenberger (29) *stratum cellulare*. This is about 0.5 mm. in thickness. In this area one finds numerous fibroblasts, scattered lymphocytes, a few polymorphonuclear leukocytes, and a finely arranged network of connective tissue through which numerous capillaries may be found. (b) The outer layer is thicker, contains a greater number of connective tissue fibers and fewer wandering and lymphoid cells, but has in connection with it simple convoluted tubular uterine glands. No sub-mucosa exists. The simple columnar epithelium of the uterine glands is without cilia, which generally holds true for the surface epithelium of the mucosa. In gravid and involuted uteri, however, there may be ciliated processes projecting into the lumen, which Wall (28) regards as being only the fibrinous product of secretion. Wall's figures are here quoted for the number of tubuli at different stages in the gravid and non-gravid uterus, "The maiden uterus in two-months or older heifers, calculated on four uteri, shows 600 to 700 cross-cut tubuli per centimeter of mucous membrane in sections of 10 microns. These tubuli have an average diameter of 17 microns. The gravid uterus (three uteri) shows an average number of 100 to 150 tubuli with a diameter of about 150 microns. Within three days *post partum* there can be counted 100 to 200 tubuli with a diameter of 50 microns. The involuted uterus (six uteri) 300 to 1000, on an average about 700 tubuli—with a diameter of about 17 microns."

It may thus be seen that the tubuli grow very large during pregnancy, but regain more or less of their former size in the involuted uterus.

The muscular coat is composed of an inner circular layer of unstriated muscle, and an outer longitudinal layer, beneath the serosa. These fibers are much enlarged in the gravid state of the uterus. The fibers interlace closely, are disposed in bundles or layers, and are intermixed with areolar tissue, containing a large number of blood vessels, lymphatics, and nerves. The areolar tissue is more abundant near the outer surface.

The external layer of the muscular coat lies directly beneath the serosa. A large number of muscle bundles begin as longitudinal bands in the cervix and are continued through the cornua and eventually pass off into the uterine tubes. The inner muscular layer and the point of ramification of the blood vessels before they pass into the mucosa serve to mark off the mucous membrane from the muscular coat proper. The width of the muscular coat is from 1.5 to 6 mm.

The serosa is a special investment of the peritoneum, consisting of a layer of flattened endothelial cells, supported by a thin elastic membrane. It shows but few alterations in the evolution and involution of the uterus.

In structure the cervix is similar to the uterus. The mucosa is free of glands (in this respect differing from the human cervix) and is much plaited by longitudinal folds, so that in cross-section it appears as a mural crown. The mucosa of the cervical canal is also thrown into transverse circular rugae, three or four such folds being present. The epithelium is for the most part single and low columnar, except that of the *os uteri externum* (*portio vaginalis uteri*) which is covered by a stratified ectodermal epithelium, as seen in the vagina. "In old cows this may spread forward 4 cm. in front of the *os uteri externum* by "ectodermoisering." Altho no cervical glands exist, its epithelium, through the presence of goblet cells, secretes a mucus, having an important rôle to play in the formation of the seal in pregnancy. The folding of the epithelium adds much surface for mucous secretion. The muscular coat is very dense and thick, the circular fibers being much more abundant than in the body or horns of the uterus. The serosa, where existing, is similar to that seen at other portions, previously described.

The arteries of the uterus and cervix are derived from the uterine and the uterine branch of the utero-ovarian, and the internal pudic. Veins accompany the arteries. Lymphatics are numerous and drain toward the internal iliac and lumbar lymph nodes. The nerves are derived from the pelvic and uterine plexuses.

4. UTERINE TUBES

The ovaries are regarded as glands for the production of ova, and the UTERINE TUBES (*tuba uterina*) represent their ducts. They do not start immediately at the ovaries, but open up into the peritoneal cavity near the ovary where they present a small orifice surrounded by their fimbria. The fimbria comes into close relationship with the ovary and may be attached at one end. When the ova are discharged they fall upon the fimbria and are transported through the lumen of the uterine tube to the uterus. At the uterine end of the tube its communication is reduced somewhat in size, forming the isthmus. Between the isthmus and the fimbriated extremity is the ampulla (near the fimbriated end).

In the bovine species, the tube is thin and tortuous and is supported by a specialized peritoneal reflection. Its entire length is from 21 to 28 cm. At the isthmus the thickness varies from 0.8 to 1 mm. and at the ampulla is from 3 to 5 mm. in diameter (29).

The uterine tube shows, microscopically, three layers: The *tunica mucosa,* the *tunica muscularis,* and the *tunica serosa.* The mucosa is supported by a *tunica propria* or basal membrane and is thrown up into folds, projecting for a greater or lesser distance into the lumen of the tube. In the bovine species these plicae vary in number from 20 to 40. The epithelium, which is supported by the stroma of the *tunica propria,* is simple (or pseudostratified), ciliated, and high columnar in type. It covers the mucosa throughout the length of the tube. The *tunica muscularia* is composed of both circular and longitudinal fibers of plain muscle. The circular layer is much the stronger and is located nearer the lumen of the tube. The longitudinal fibers are seen external to the circular and are less developed. The muscularis is strongest near the uterine end of the tube. The serosa is a specially reflected portion of the peritoneum (serous mesothelium) which covers the external portion of the tube, forming its *tunica serosa.*

The ARTERIES are derived from the utero-ovarian, and the veins are satellites of the arteries. The lymphatic vessels pass with the ovarian vessels to the lumbar lymph nodes. The nerves come from the sympathetic, renal, and aortic plexuses.

5. OVARIES

The OVARIES are two small, oval, somewhat solid looking bodies, lying one on each side of the pelvis, and projecting into the peritoneal cavity at the posterior part of the broad ligament, which is itself formed by a fold of peritoneum. During sexual life a number of clear vesicles can be seen near the surface of the ovary, sometimes even projecting beyond the surface. These are the ripe or ripening Graafian follicles.

There may also be seen occasionally one or more yellow masses imbedded in the ovary, the *corpora lutea.* These may project slightly from the surface of the ovary, in the form of a small rounded elevation. Their dimensions on the average are 1½ to 2½ cm. in length 1⅓ to 2⅔ cm. in breadth, 1⅓ to 1½ cm. in thickness, with a weight of from 10 to 15 grams. The right ovary is slightly larger than the left (30).

Each ovary is formed of a solid mass of fibrous looking tissue, which contains between its fibers very many elongated cells, like those of embryonic fibrous tissue. The stroma is more condensed near the surface where it forms the *tunica albuginea.* The ovary projects into the peritoneal cavity, but is not actually covered by a serous membrane. The peritoneum ceases abruptly at the attachment to the broad ligament. Along this line of attachment (hilum), blood vessels and nerves enter and leave the ovary. In this location frequently are seen a large number of interstitial cells, much like those seen in the testis. Similar cells may occur scattered in groups about the stroma, but do not seem to be numerous in the bovine ovary. A layer of short, clear, columnar epithelial cells (the germinal epithelium) covers the entire clear surface of the ovary. Primitive ova may occur among them. Here and there, especially in the young animal, the epithelium is thickened and dips into the stroma of the ovary. These have been described in the embryology of the ovary as Pflügers egg tubes (or cords). In the development of the ovary these cords become broken up into islands of epithelial cells, from which the Graafian follicles arise. Imbedded in all parts of the cortical stroma, except near the hilum, are a large number of spherical or ovoid vesicles, each containing an ovum, together with other cells. These vesicles are the Graafian follicles. They are of all sizes ranging from the size of the ovum, and entirely microscopic, to 15 mm. in diameter. The smallest Graafian follicles contain only a small ovum and a single layer of epithelial cells surrounding it. The largest contain an ovum of mature size (about 0.2 mm. in diameter) surrounded by a considerable mass of epithelial cells, known as the *cumulus oöphorus,* by which it is attached to the wall of the follicle. Layers of the same cells line the wall continuously, and constitute the *stratum granulosum.* The wall itself is fibrous and known as the *theca folliculi.* The large follicles are distended with a clear, straw-colored fluid, the *liquor folliculi.* As the fluid accumulates the follicles project from the surface as little convex, translucent elevations. It is at this point that the follicle eventually bursts, liberating the ovum surrounded by its *cumulus oöphorus.* The *stratum granulosum* remains *in situ* and undergoes proliferation, developing into the epithelial tissue

of the *corpus luteum*. The smallest Graafian follicles (primary follicles) are found near the surface of the ovary, in the so-called cortical layer. As the follicles develop they sink into the stroma, and as they become enlarged through the elaboration of their *liquor folliculi* (probably secreted by the *membrana granulosa*) again approach the surface. Many follicles never go beyond the primary follicle stage but after a time undergo a degenerative change by either atrophy or atresia of the follicle. The *theca folliculi* undergoes growth and organization, finally replacing the follicle. These are known as atretic follicles. The ova are large spherical cells with clear nuclei and large nucleoli. They are enveloped by a clear membrane known as the *zona pellucida*. The ovum is composed of clear cytoplasm, the vitellus, a large vesicular nucleus, the germinal vesicle, within which is a single dark staining nucleolus, or germinal spot. The cytoplasm (vitellus or yolk) contains many granules, especially near the central part. The nucleus (germinal vesicle of Purkinje) measures about 0.05 mm. in diameter. Following the rupture of the Graafian follicle and the escape of the ovum, there is considerable hemorrhage. This blood clots in the former cavity of the follicle and gives rise to the *corpus rubrum*. The follicular wall begins, almost immediately, to hypertrophy and is thrown up into folds or plaits. The greater part of the hypertrophy is from a thickening and proliferation of the epithelial cells of the *stratum granulosum*, followed by inward growth of vascular processes chiefly from the *theca folliculi*. The *corpus rubrum* undergoes dissolusion and absorption before this advancing growth, which when completed is known as the *corpus luteum*. The cells of the *corpus luteum* are known as lutein cells, and grossly appear to be yellow. The pigment is for the most part carotin with small amounts of xanthophil (31).

The *corpus luteum* is at first sharply marked off from the surrounding ovarian stroma, by the *theca folliculi*. After a time it becomes less sharply differentiated from the stroma. The lutein cells undergo absorption, and connective tissue replacement which later becomes contracted and subjected to hyaline changes. Thus in ovaries of aged animals white scars are prominent throughout the stroma, which often even cause an irregular scarring of the ovarian surface. These remains of the *corpora lutea* are known as *corpora albicantia* or simple sclerotic *corpora lutea*.

The arteries are derived from the ovarian arteries which are large and flexuous and reach the ovary by passing between the layers of the mesovarium. Veins are large and numerous. Lymphatics drain toward the lumbar nodes. Nerves are derived from the sympathetic system through the renal and aortic plexuses. The vessels enter the ovary at the hilum.

6. ATTACHMENTS OF THE GENITAL ORGANS

The body and cornua of the uterus are attached to the abdominal and pelvic walls by two extensive peritoneal folds, the broad ligaments (*ligamentum lata uteri*). These extend on either side from the upper part of the flanks, about a hand's breadth below the level of the *tuber coxae*, to the dorsal border of the cornua and the lateral margins of the body of the uterus. They contain the blood vessels, lymphatics, and nerves of the uterus and ovaries, connective tissue, and a considerable amount of unstriped muscle which is continuous with the smooth muscle of the uterus. The ureters are situated along their parietal margins. The lateral layer of each gives off a fold, the round ligaments of the uterus (*ligamentum teres uteri*), which blend with the parietal peritoneum, and can be distinctly traced to the vicinity of the abdominal inguinal ring. The anterior extremity of this ligament is situated above the extremity of the cornu, and forms a long, round appendix. It contains muscle tissue, vessels, and nerves, and is the homologue of the *gubernaculum testis*. The anterior part of the neck is continuous with the vagina, and thus has a more fixed position than the rest of the organ.

DEVELOPMENT AND STRUCTURE OF THE FETAL MEMBRANES

Fertilization of the ovum usually occurs in the isthmus of the uterine tube, after which the ovum descends into the uterus, sometimes during the first week of pregnancy, still surrounded by its *zona pellucida*.

Upon arrival of the fertilized ovum in the uterus, the condition of that organ is typical of that of the unimpregnated organ (to be described later). The glands contain very little secretion and no trace of blood or debris. The stroma cells increase in number and become more dense, leukocytes begin to invade the epithelium. The ovum soon becomes implanted in the uterine wall, and the fetal membranes develop about it. A destruction of the uterine epithelium begins about this time (18 days) over the carunculae, and extends to all parts of the uterus that are in contact with the growing embryo. Regeneration of the epithelium over the carunculae does not occur until after parturition, while over the intercotyledonary areas (the gland mucosa) regeneration takes place about the third month of pregnancy.

About the fertilized ovum there develop, soon after conception, certain appendages. These are: (1) The chorion, with the *placenta fetalis*, (2) the amnion, and (3) the allantois. These serve to protect the fetus and to carry maternal nourishment to it.

"The CHORION (or vascular membrane) is the outer envelope surrounding the foetus and the two inner membranes, and adapts itself closely to the outer surface of the mucous membrane of the uterus."

(22) . Its development permits it to extend into the non-impregnated horn and *corpus uteri*. On its external surface there are tufts of villi which constitute the fetal cotyledonous placenta. The chorion arises partly from the superficial layer of the morula (ectoderm) and partly from the embryonic parietal mesoderm, which develops later. The trophectoderm forms the outer layer of the blastodermic vesicle, which internally is made up of a mass of cells. The trophectoderm forms the primitive ectodermal layer of the chorion, which is composed of a single layer of cuboidal epithelial cells, and several ovoid binucleated cells. The former probably correspond to Langerhan's layer of the human chorion, the latter to the syncytium. These represent the growing elements of the chorion, the chorionic villi. The mesoderm gives rise to a connective tissue stroma supporting the ectodermal layer, which also accompanies the trophoblast of the villus, forming a connective tissue core, or supporting stroma. The villi grow into the swollen carunculae and this union constitutes the fetal and maternal placenta. The exchange of nutritive material takes place between the fetal placenta and the mother through absorption and imbibition of maternal juices. There is no direct communication between the maternal and fetal circulations. The chorionic villi approximate the large vessels of the carunculae and obtain for the fetus materials essential to its life. The fetal blood vessels follow the stroma of the chorion and thus (as they arise from the allantois) the blood-borne waste products of fetal metabolism are also eliminated and taken up by the maternal uterine circulation. In ruminants the chorion is united to the amnion and allantois over the middle of its inner surface, by loose gelatinous connective tissue. On the surface of the cotyledons of the cow is found a fluid in the nature of an emulsion (uterine milk). It is a whitish or reddish emulsion of alkaline or neutral reaction, with a specific gravity of 1.036. Gamgee (22) found in 1000 parts of uterine milk: Water 879.1 parts, solids 120.9 parts, the latter being represented by albumin (with the cells) 104 parts; alkaline albuminates, 1.6 parts; fats 12.33 parts; organic salts 3.74 parts; also some creatin, creatinin, and xanthin. Colin (22) regarded it as a post-mortem product of decomposition, while other experimenters regard it as possessing an important nutritive function.

The AMNION begins to develop as soon as segmentation has been completed and the ovum has reached the uterus. It appears at approximately the end of the second week of pregnancy. The development of the amnion has been traced to the external layer of the blastoderm. It begins at the umbilicus and surrounds the fetus like a sac, enclosing it entirely except at the point of origin, where it takes part in the formation of the umbilicus. It is a thin, double membrane of little resistance. In ruminants the inner surface is studded with little

yellow projecting points, called by Claude Bernard (22), "plaques glycogenique," for they are composed of glandular tissue capable of producing glycogen. In this respect it is held that this function replaces the function of the fetal liver, until that organ is developed (Joulin, St. Cyr, and Violet in "Traite d' Obsteterique"). Lecoq (22) holds that they are simply changed parts of the fetal skin. They are most numerous about the amniotic portion of the umbilicus. The external surface of the amnion is partly in contact with the allantois laterally and at the back of the fetus with the face of the chorion. The inner of the two membranes, previously mentioned, constitutes the true amnion, while the external one forms the external or false amnion, which by fusion replaces the prochorion, thus forming the primitive chorion. Later when the allantois grows out it blends with it to form the permanent or allantoic chorion. This outer or false amnion is merely a portion of the external wall of the blastodermic vesicle, without having had its relations changed exteriorly. The space between the amnion and the fetus constitutes the amniotic cavity and is distended with a clear straw-colored fluid. It is oval in shape with a depression at the umbilicus, thus giving to it a kidney or bean shape. As it becomes filled with fluid and enlarges it invests the vitelline stalk and allantoic cord in its passage through the cavity. In the latter part of pregnancy the fluid becomes mucoid, opalescent, and stringy, and may contain fetal feces (meconium), giving it a brownish tinge. The amount of amniotic fluid at birth averages 4 kg. It serves a mechanical function, protecting against injury and lubricating the vagina during parturition.

The ALLANTOIS arises as an invagination from the hind gut, just posterior to the vitelline duct, and grows outward and backward between the two amniotic layers (or if considered as by some authors, between the chorion and amnion). It is a continuation of the urachus and is sacular in shape, from which it receives its name, allantois (Gr. sausage). The urachus forms a tube for communication between the allantois and urinary bladder of the fetus. The external face of the allantois rests on the internal face of the chorion. When the allantois is isolated and emptied it is seen by inflation to be a bicornual, irregular, cylindrical sac, the head of the fetus lying in the shorter cornu, the posterior extremities in the larger. The allantoic sac contains the allantoic fluid (the fetal urine), which gradually accumulates. It is a whitish foamy, thin fluid of neutral reaction, which later in pregnancy becomes yellow or brownish. Near the end of pregnancy it amounts to from 8 to 15¼ liters. Robin (22) has proved the absence of glucose, oxalates, albumin, mucus, allantoidin in the allantoic fluid. The allantois is important in transporting the fetal blood vessels to the chorion, and to the chorionic villi of the placenta, where the transference

of maternal nourishment to the fetus occurs. It also acts as a reservoir of fetal urine.

Other important appendages are the vitelline or *yolk stalk,* supplying nutrition to the developing embryo until maternal connections can be obtained. It is not of importance beyond this. It arises from the primitive gut. The umbilical cord is composed of the urachus, two umbilical arteries, two umbilical veins, and the remains of the yolk stalk. All these are imbedded in a gelatinous mass, "Wharton's gelatin" or jelly. The sheath of the umbilical cord is formed from folds or invaginations of the amnion. The urachus carries the fetal urine to the allantois. The umbilical arteries supply the fetal membranes and as previously stated, through their circulating blood exchange fetal katabolic products for maternal nutritive products, in the placenta.

PHYSIOLOGY OF REPRODUCTION

THE ESTRUS CYCLE

The cycle of events leading to estrum (or heat) is known as the *diestrous cycle.* The cycle is usually divided into four states: (1) *proestrum* (period of growth and congestion, followed by the period of destruction), (2) *estrum* (beginning period of recuperation—"heat"), (3) *metestrum* (period of recuperation), (4) *diestrum* (period of rest). If conception does not occur at any estrus period during the sexual season, a prolonged period of rest may follow. This is known as the anestrous period. The latter is ordinarily shown only by certain species of animals having definite breeding seasons. The complete cycle of events, including anestrum, is known as the anestrous cycle.

The periods of proestrum and estrum are commonly referred to as the "heat period." As a matter of fact there is a marked physiological difference in these two periods, *proestrum* corresponding to *menstruation* in the human female, in which there is an increased activity of the uterine glands resulting in congestion of the uterus. Frequently at this time bloody or clear mucus containing polymorphonuclear leukocytes and other white blood cells can be seen coming from the glands, followed by epithelial destruction and bleeding. The amount of blood is slight in the cow, but is commonly seen in the vagina. In sheep, where careful studies have been made, bleeding is a well established fact. This corresponds to the menstruation of the human female but is much less marked. The period lasts from 2 to 4 days as a rule. The *proestrum* is a process preparing the uterus for implantation of the ovum in its wall and corresponding as it does to menstruation probably does not occur as Williams states (26), based on clinical evidence, after the *estrum,* but before, as was pointed out by Heape (32)

and later by Marshall (33). Any other conclusion would make it necessary to change our entire conception of the physiology of *proestrum* or menstruation.

Proestrum is followed by *estrum* which is of very short duration. It marks the climax of the estrous cycle. At this time the female is willing to take the male and fruitful coition is possible. The uterus is in the beginning of recuperation, the glands are less active, hyperemia subsides and healing has commenced. Large numbers of leukocytes can be seen in the stroma. Some are phagocytic for the cellular detritis and blood pigment remaining from the proestrus.

If conception occurs, this period is followed by the *period of gestation*, which in the bovine species has an average duration of 275 days.

On the other hand, should conception not occur during estrus, the latter is succeeded by a short *metestrum*, during which activity of the generative organs subsides and they gradually return to normal.

In some animals the *metestrum* may be succeeded by a long period of quiesence, the *anestrum*, while in others it is followed simply by a short period of rest. This interval is known as the *diestrum*. Following this period of rest, *proestrum* (period of growth and congestion followed by period of destruction) again begins, and the diestrous cycle is complete. It is probable that the uterine changes do not take place abruptly, but that each day marks certain differences in the progress of the cycle. The latter has been well studied in the human female and in the apes, where a menstruation similar to that in woman occurs. In primates the cycle may be divided into four stages:

(1) The stage of construction   (3) The stage of repair
(2) The stage of destruction   (4) The stage of quiescence

The completion of the diestrous cycle in cattle, according to Ellenberger (63) varies from two to four weeks. Wallace (57) states that in summer estrus occurs among cattle every nineteen days, but in winter every twenty-one or twenty-two days. After parturition the cow usually appears to be in heat again within four or five weeks. The domestic cow is polyestrous, having several recurrent breeding periods at more or less regular intervals each year.

THE OVARIAN FACTOR IN REPRODUCTION

Through continued experimental evidence it has been adduced that the diestrous cycle is definitely controlled through the activity of the ovary. Heat and menstruation are brought about by the elaboration of some sort of chemical substance or hormone, having its source in the ovarian tissue. This so-called internal secretion, not only controls the functional activity of the uterus, but also has to do with the

development of the mammary glands and other sexual characteristics of the female.

The earlier view of Pflüger that the functional correlation between ovary and uterus was through the nervous mechanism, is no longer tenable (34). Neither is the occurrence of menstruation connected with the ripening of the Graafian follicle, for Heape has shown that in monkeys menstruation may occur in the absence of either ripe Graafian follicles or *corpora lutea* (32). It has also been noted that in bats copulation occurs in the autumn, and ovulation is not observed until the following spring, the spermatozoa being stored in the uterus during the period of hibernation. It can thus be seen that the Graafian follicle can have little to do with estrum. Fraenkel (35) has stated that menstruation is brought about by the effect of an internal secretion elaborated by the discharged follicle or *corpus luteum*. He also regards the *corpus luteum* as the only ovarian organ of internal secretion and as being responsible for the estrus cycle as well as the raised nutrition of the uterus during pregnancy. Fraenkel regards the fact of its recurrence following the menstrual period in women, and its monthly regeneration as proof of the importance of the *corpus luteum* as an organ of internal secretion. This, like the above theory, is held by Marshall (34) to be untenable, because it will not account for the sexual phenomena in the lower animals. Most animals ovulate when proestrum is over, so that the *corpus luteum* is usually not present when estrum or "heat" begins. Further proof exists in the female rabbit and cat where ovulation occurs only after copulation, and in the absence of the male, *corpora lutea* are not formed in the ovaries, yet these animals show periodic heat periods.

To summarize all these facts it seems, as Marshall states, the proof of "heat" can not lie in the internal secretion elaborated by the *corpus luteum*, but the theory does seem to explain the raised nutrition of the uterus during gestation, and also is a determining factor in the development of the mammary glands and in the continued existence of the fetus in the uterus at least during the early period of pregnancy. Marshall (34) has shown that "heat" is not dependent upon the development of the Graafian follicle nor upon the *corpus luteum* and suggests that its occurrence must be accounted for by the secretion from the interstitial cells, altho no proof can be adduced showing cyclic changes in these cells. Marshall states further that, "The ovary is an organ providing an internal secretion which is elaborated by the follicular epithelial cells or by the interstitial cells of the stroma. This secretion circulating in the blood induces menstruation and heat. After ovulation, which takes place during estrum, the *corpus luteum* is formed, and this organ provides a further secretion whose function

is essential for the changes taking place during the attachment and development of the embryo in the first stages of pregnancy." It is probable also that it is intimately concerned, through its internal secretion, with the development of the mammary glands, and that the hormone elaborated by the ovarian stroma has to do with the maintenance of the general metabolic equilibrium, and the development of female secondary sexual characteristics. The rôle of the ovary in influencing the general metabolic state has long been known. It has an intimate relation with other glands of internal secretion, changes in one of which seem to derange the others. The possibility exists that this latter function resides in the *corpus luteum,* but definite evidence of its function in the ovary is still unknown.

That *corpora lutea* do not play an important rôle in the estrus cycle is shown, too, by the fact that they are not present during proestrum, and as ovulation occurs in either late proestrum or estrum, they can be functional only subsequent to their appearance, that is, after ovulation. Fraenkel maintains that the *corpus luteum* of the previous ovulation induces estrum of the succeeding one, but as a matter of fact, the previous *corpus luteum* has generally degenerated into the albicans before the succeeding ovulation appears. Further proof lies in finding that in certain animals estrum and ovulation do not necessarily occur simultaneously. It is a well-known fact that in cows *corpora lutea* retained pathologically cause cessation of estrum and of ovulation, and that the removal of the *corpus luteum* by manipulation per rectum, will within from 3 to 7 days cause the appearance of heat, and the animal may conceive if bred at this time (36). It seems, therefore, that this is additional proof of Marshall's theory that the ovarian secretion having control of estrum and ovulation must be sought for in other portions of the ovarian tissue. The lutein tissue, it would seem, inhibits ovulation, which may be another function of that body during pregnancy when both ovulation and heat are inhibited. Pearl and Surface (37) have shown that extracts of *corpus luteum* when injected into laying hens inhibit ovulation, a further support of the inhibitory action theory of the lutein secretion. Inhibition may be the result of mechanical blocking, but more likely the active secretion of the *corpus luteum* inhibits the ovarian function (or the ovarian secretion) controlling estrum and ovulation, for, as previously stated, its removal when pathologically retained causes estrum to appear. It is also possible that its secretion, if controlling estrum as Fraenkel states, is only elaborated in the period of its regression, a fact which would correspond to the cyclic changes that actually appear. The lutein secretion being most abundant during the latter stages of the regression of the *corpus luteum,* would correspond to

the phenomenon of menstruation, which in itself might be responsible for the phenomenon of heat appearing after the proestral or menstrual state. The climax reached, the uterus undergoes a period of rest and repair. During this period a new *corpus luteum* is formed from the ruptured follicle and as it regresses begins to secrete. Thus the cycle recommences. This is hypothetical and probably not what actually occurs, for Marshall points out that heat appears regularly in rabbits in the absence of the lutein cells.

The entire consideration must be only theoretical until the active principles of the internal secretions of the ovaries and *corpora lutea* can be isolated chemically and definitely separated. The fact remains, however, which is the important thing, that the ovary has internal secretions intimately connected with developmental and sexual changes.

CLASSIFICATION OF STERILITY

No thoroly workable classification of sterility of animals, from a pathological viewpoint, exists. From the clinical standpoint an animal is sterile when she no longer produces young, but the causes are so diversified and prognoses likewise so variable that a fundamental classification is difficult when based upon etiology and pathology. Many authors regard sterility as a symptom of disease, or when no demonstrable reason can be adduced for the condition, as an entity in itself.

The basis for the first subdivision is sex: (1) due to the male, (2) due to the female. This report is confined exclusively to the latter. A further subdivision of either (1) or (2) might be adopted as follows: (a) Congenital (usually absolute), and resulting from absence or arrested development of certain organs of reproduction. Congenital displacement, altho rare, may also be a contributing factor. (b) Acquired (relative or absolute), and the result of (1) acquired displacements or injuries, (2) tumors or cysts, (3) specific inflammations, (4) non-specific inflammatory reactions.

GENERAL CONSIDERATION OF STERILITY

Sterility may be said to result, as a rule, when there are deviations from the normal in the genitalia. Factors which are considered essential to conception are: (1) a normal ovum; (2) healthy and active spermatozoa; (3) normal tubal, uterine, and vaginal secretions and structures; (4) a healthy endometrium in which the fertilized ovum may lodge and develop. Inability to produce young is normal before puberty and in aged cows, also occasionally in healthy lactating animals. Gebauer (38) suggests that cows be regarded as sterile (1) when they have passed their second year without showing signs of estrum; (2) in

stables where sterility is prevalent when cows show no signs of estrum for a period of 8 weeks; (3) when after calving estrum has not appeared within two months.

CONGENITAL DEFECTS OF ORGANS OF REPRODUCTION

Complete absence of the ovaries is rarely met with, while arrested development, altho not common, is more frequently seen. In bovine twins, sexual development is often arrested (90 per cent of cases according to Williams (26) when the twins are of opposite sex. These heifers, for the incomplete development almost always occurs in the female, are known as freemartins. Such individuals are absolutely sterile, unless the defect is a minor one. As a rule the arrest in development leaves the animal without uterus or with one only partially formed, or without a normally developed vagina. These animals are unquestionably sterile. In other cases where only minor defects of the uterine tubes, uterus, or ovaries exist, conception may occur. This arrest in development is sometimes seen in heifers not of twins. We have studied two cases in this work in which arrest in the development of uterus and vagina existed. There were in place of the uterus only partially developed horns and fibrous cords, the remains of the Müllerian ducts. These will be described in detail later. Thus we may have complete absence of any essential organ of reproduction or arrested development. Whether the animal will be sterile or not depends upon the extent of involvement.

DISEASES OF THE OVARIES

A. ACTIVE and PASSIVE HYPEREMIAS and ANEMIAS may occur but are not important from the standpoint of sterility. Active hyperemia occurs in estrum and in infections, the passive type when a general passive hyperemia exists (or locally when venous blood flow is in any way obstructed or retarded). Anemias exist in a general anemic state, and because of obstruction of arterial flow.

B. CYSTIC CHANGES are among the most frequently encountered diseases of the ovaries. Zangger (39), in 1859, seems to have been the first to study this condition. Since then, Hess, Albrechtsen, and Williams have contributed to our knowledge of the condition in cattle.

Ovarian cysts may be divided pathologically as follows:

    1. Simple ovarian cysts (retention cysts)
        a. Originating from the Graafian follicle.
        b. Originating from the *corpus luteum*.
        c. Originating from the remains of the Wolffian ducts.
    2. Pseudomucinous cystadenomata.
    3. Serous cystadenomata.

Pathologists are not agreed on a pathological classification of ovarian cysts. Some hold that they all have a common origin from tubular ingrowths of epithelium. Most workers favor a division into: (a) Retention cysts, (b) cystic neoplasms. Retention cysts may be of three types: (1) Failure of the Graafian follicle to develop normally or failure to rupture with subsequent failure of the *corpus luteum* to form. Thus the follicle becomes distended as a follicular cyst. (2) Cystic degeneration of the *corpus luteum*, at any time during its development, but usually when pathologically retained. (3) Another type of retention cyst is seen especially at the hilum or on the broad ligament. These form from cystic remains of the Wolffian duct and attain a great size. This type is infrequent in cows.

Superficial follicular cysts can not be distinguished grossly from normal follicles except that they are larger than the ripe follicle, but size alone is no criterion. Often they are small and multiple. Again they may be large and single. Frequently too, ovaries containing one large cyst and two or three smaller ones are noted. These cysts vary in diameter from microscopical size to 18 to 25 mm. (or more), the average being between these extremes. They are thin-walled when occurring superficially, but the walls are thicker when in the deeper ovarian structures. The epithelium, which is always in part retained in the follicular cysts, becomes stretched and flattened and lies on its basement membrane. The cavity contains a straw-colored serous fluid, usually thin but often mucinous with or without the presence of the ovum (usually without). Sometimes the Graafian follicle only partially develops and then begins to degenerate. The *stratum granulosum* may be partly destroyed. The cavity is always distended with fluid, which microscopically appears as a dense homogeneous eosin-staining mass. Such cysts may be small and multiple or may enlarge to great size. These will be described in detail in the case reports.

Corpus luteum cysts are similar in appearance, except that in place of follicular epithelium around the inner wall, lutein cells and connective tissue are always found. The fluid is often darker in color and may even be blood stained. It is usually thin, but in one of our cases it was of a thick, gelatinous consistency and yellow in color.

Embryonal remains of the Wolffian ducts are occasionally cystic but are very infrequent in cattle. They are most often found on the broad ligament.

The cystadenomata are not often described in veterinary literature and are therefore of little importance in sterility. Kitt (40) reports them as developing to the size of 20 to 30 or even 90 kilos in weight in the mare and cow. They are true neoplasms arising from continued ingrowths of either Pflügers egg cords or superficial ovarian germinal

epithelium. This ingrowth ordinarily is not continued after birth, but when it occurs it gives rise to these adenomatous structures. Cavities lined with simple cuboidal epithelium supported by a connective tissue stroma is the characteristic picture presented. The growth of epithelium spreads from the parent cyst. Daughter cysts are thus produced until a multilocular arrangement is formed. The epithelium secretes either a serous fluid or a pseudomucinous one, quite jellylike in consistency. Either simple or papillary arrangement of the epithelial lining may be the typical appearance. When completely removed the cystadenomata do not recur, neither do they metastasize, but grow from the original focus, along the abdominal peritoneum until eventually they may approximate the border of the liver. In some instances they give rise to carcinomata. It is probable that cysts may also be formed from the structures just described without exhibiting any marked neoplastic characteristics, but there is always a potential growth impulse in their make-up.

The etiology of retention cysts is not known. Rosenau and Davis (41) have associated *Streptococcus viridans* with cystic disease of the ovaries of women. Fitch (42) in his studies found streptococci and *B. coli* in cystic ovaries. Loeb (43) has been able to produce cysts by underfeeding guinea pigs. Only by excessive underfeeding was he able to produce the condition, and then with considerable regularity. Ewing (58) states that the "Fairly constant occurrence of inflammation of the pelvic organs points to the inflammatory origin of these cysts." It is possible that abnormal conditions or infections of the uterus exert a reflex influence upon ovarian function with, possibly, cysts as one of the ovarian changes produced. In regard to etiology of cystadenomata we know nothing more than that they are neoplasms, arising probably as has been suggested.

The symptoms produced by cystic ovaries are usually those of nymphomania. Frequent and irregular heat periods, usually with inability to conceive are often observed, because of abnormal ova or absence of ovulation. Absence or suppression of estrum is sometimes seen as a sequel to cystic ovaries.

C. PATHOLOGICAL RETENTION OF THE CORPUS LUTEUM is often noted. It has no special pathology, simply a retention and hypertrophy of the "yellow body," which for some unknown reason fails to degenerate into the *corpus albicans*. Its retention frequently results in suppression of ovulation and estrum. If estrum occurs, copulation is seldom followed by conception. Usually after some months, the *corpus luteum* becomes encapsulated within a firm connective tissue wall. The lining cells are connective tissue, within which are lutein cells, the remains of the *corpus luteum*. The etiology is unknown

D. Sterility may result from a general DERANGED METABOLIC STATE through the influence it may have upon the ovary. Glands of internal secretion have been demonstrated as playing an important part in the physiological development of the female, and in general body health. Overwork, insufficient food, high protein diet, obesity, and emaciation all render the ovary less responsive and sometimes result in temporary sterility or weakened and irregular estrum.

E. OÖPHORITIS.—Inflammations of the ovary are acute or chronic. The acute types are most often associated with abscess formation from extension of peritonitis, perimetritis, or salpingitis. The chronic types produce proliferative changes with resulting scars and adhesions. The causes may be tuberculosis, actinomycosis, or pyogenic infections produced by streptococci, staphylococci, or *Bacillus pyogenes*. The infection usually enters the ovary following rupture of a Graafian follicle. Sterility produced thereby is almost always absolute.

F. TUMORS.—Both carcinomata and sarcomata are rarely primary in the ovary, the former being the most common. Dermoid cysts and teratomata are also not infrequently seen, but in cattle are rare. The presence of such growths results in loss of ovarian function with or without symptoms of nymphomania, and in sterility. The cystadenomata have been previously described.

G. SENILE ATROPHY OF THE OVARY is normal in old animals. The rupture of each follicle leads to the development of a *carpus albicans*. This is simply a scar which remains as a result of degeneration and fibrous replacement of the *corpus luteum*. With increasing years these gradually accumulate and undergo hyaline degeneration so that in ovaries of old cows the surface will be seen studded with scars, the *corpora albicantia*. Primitive ova become exhausted or cease to develop into mature follicles. This we speak of as senile atrophy, and representing as it does loss of ovarian function, produces sterility. The period in the animal's life at which this change occurs is not definitely set as in the human, for so far as is known animals do not pass through the menopause. Sometimes the early development of senile changes results in sterility from atrophy in young animals.

H. It is not infrequent to see sterility in cows, with suppressed or feeble estrum, irregular periods, or even complete absence of estrum, when on careful necropsy NO EVIDENCE OF DISEASE, either gross or microscopic, can be found in any organ. Some of these, it is suggested, result from derangement of the endocrines, others are possibly the result of reversion upon the part of the animal to the wild state where estrum in the "Ungulata" occurs but once a year. Suppressed estrum may be an expression of the long anestrous period common to the species before domestication. Marshall (33) cites the observation

that wild monoestrous animals belonging to the same order in the kingdom as the bovine species, when placed in captivity change to polyestrous types, through change in habit. If this is true, reversion in the other direction, influenced by physical factors, is also possible and may explain long continued absence of estrum in some animals when no other cause can be adduced.

DISEASES AND AFFECTIONS OF THE UTERINE TUBES

The importance of diseases and defects of the uterine tubes in relation to sterility can not be overestimated. It must be kept in mind that the uterine tubes are the ducts of the ovaries and the ova must pass through them in order to reach the uterus. It will be remembered that their lumen is narrow, their structure delicate, and their mucosa thrown into folds, directed toward the center, so that injuries, altho slight, may result in temporary or permanent sterility. One normal tube is all that is necessary for conception but, as a rule, infections are bilateral, thus rendering both sides impassable to ova. It is said that simply the loss of cilia from the epithelium is sufficient pathologic change to produce sterility.

A. Senile changes, or atrophy of the tubes, are normal in aged animals (in women after the menopause). The chief characteristic of the change is atrophy, the tubes becoming smaller. Atrophy frequently results from pelvic adhesions, brought about by infections and pelvic tumors. It may also result from impaired circulation secondary to ovarian cysts, or degenerative changes in the intima of arteries and arterioles supplying the tubes.

B. Circulatory disturbances are:
    1. Anemias, from local obstruction or a general anemic state.
    2. Hyperemias
        (a) Active, during estrum and resulting from infection.
        (b) Passive, occurring as a result of obstruction to return flow of blood, general congestion, thrombosis of the ovarian veins or tumors pressing upon them.

In active hyperemias due to infections we have the only circulatory disturbance of any importance in sterility. The typical picture of inflammation is produced. In passive hyperemias the tubes appear blue, the typical picture of retarded outflow of blood.

C. Hematosalpinx, the accumulation of blood in the uterine tubes, occurs as a result of tubal pregnancy, or twisting of the tube resulting in passive congestion and tubal hemorrhage. Such twists may be produced by ovarian tumors and ovarian cysts. It may result in rupture of the tube with fatal hemorrhage, or the clot may undergo organization,

thus destroying the function of the tube through stenosis. Tubal pregnancy is rarely seen in the bovine species.

D. ACQUIRED DISPLACEMENTS may be seen, as torsion or adhesions of the tubes. These frequently follow torsion of the uterus, ovarian tumors or cysts, adhesions brought about by parauterine infections or other inflammatory reactions, such as are produced by peritoneal tuberculosis. Adhesions may occur without torsion and occlude the duct, thus rendering the lumen impassable to ova. In these, most often bacterial infections are the cause, and the changes seen are for the most part similar to those described for chronic salpingitis. Many times as a result of ovarian cysts the tube undergoes torsion near the ampulla. This results in occlusion of the duct, and the tubal and ovarian secretions (from ruptured cysts) are dammed up behind the stenotic portion. Thus by close adhesion to the ovary, tubo-ovarian cysts are formed. The importance of displacements of the uterine tubes to sterility, lies for the most part in the possibility of bilateral involvement.

E. INFLAMMATIONS OF THE UTERINE TUBE are known as salpingitis. When involving the mucosa, they are designated endosalpingitis; the mucosa and muscularis, simply as salpingitis; and when involving the serosa, perisalpingitis. It is rare that the mucosa alone is attacked, probably only in the early stages of inflammation is it seen independent of deeper involvement. Perisalpingitis may occur from within outward, or by extension from the abdominal osteum of the tube. Very frequently it follows parametritis and perimetritis, with resulting adhesions and displacements as already described. Extension of tuberculosis may also be a cause. Salpingitis is by far the most frequent and most important condition seen in the uterine tubes. It may be divided into acute and chronic catarrhal salpingitis, and acute, subacute, and chronic purulent salpingitis.

Etiology. In the bovine species, as in woman, it may be said that salpingitis occurs only as the result of bacterial infection, the most common invaders in cattle being *Bacillus pyogenes* (Lucet) and streptococci, with staphylococci usually present but playing a secondary rôle. Salpingitis very seldom occurs acutely, except as a result of puerperal infection, but may occur (as in one of our cases) by extension of pyometra in a virgin heifer. The relation of *B. abortus* to salpingitis is merely as a predisposing factor, preparing the way for pyogenic infection of the uterus, with a secondary salpingitis. It may rarely result from the extension of peritonitis or pelvic abscesses. Theoretically, salpingitis may be primary and of hematogenous origin, but practically this never occurs. Salpingitis is often bilateral.

The results of salpingitis are (1) permanent damage, and (2) no permanent damage to the tube. Its extension to the peritoneum often causes peritonitis, either localized in the pelvic region with formation of large abscesses or generalized. Fusion with the ovary not infrequently results in the formation of large tubo-ovarian abscesses. Then, too, it may heal in the incipient stage and complete recovery result.

1. Catarrhal salpingitis occurs acutely as a preliminary stage in the course of inflammation of any mucous membrane and is most of the time not the stage of inflammation resulting in serious damage. It is a transitory outpouring of mucus seen in the congestive stages of inflammation. Gillman (44) has described chronic catarrhal salpingitis as producing productive inflammatory changes in the tubes with resulting stenosis and hydrosalpinx. Organisms may be of sufficiently low virulence to produce such changes, but it seems more likely that most of the chronic changes result from old purulent infections. In catarrhal salpingitis lymphocytes are the predominating cells in the inflammatory exudate, rather than polymorphonuclear leukocytes. The process and changes are similar to those described for chronic purulent salpingitis. It is a low-grade chronic type of inflammation from the start.

2. Purulent salpingitis may be conveniently divided into acute, subacute and chronic. The subacute stage is an arbitrary division to indicate the gradual progression into the chronic type.

The acute form is ushered in by the ordinary inflammatory reactions, congestion, edema, and exudation. As is true of inflammatory reactions on all mucous surfaces, the first change seen is congestion, during which time there is a serous or catarrhal exudate. In case the infection is halted here, no further change occurs, and the mucosa goes on to repair. Either healing results or the process proceeds to the next stage. The increased secretion (or catarrhal stage) is followed by exudation of polymorphonuclear leukocytes, red blood cells, lymphocytes, and plasma cells. At first few in number, they gradually increase until the exudate appears muco-purulent. The clear mucus is streaked with pus. Gradually it becomes more purulent and contains the cells and debris ordinarily seen in any purulent exudate. The tube is swollen, and distended with pus which has free drainage to the uterus. In the beginning the walls are stretched and thin, but if the process continues they become thick through organization and proliferation of highly vascular connective tissue. This results in a tortuous or kinked tube. Microscopically the lumen of the tube is seen to contain a purulent exudate, consisting of inspissated serum, fibrin, polymorphonuclear leukocytes, a few lymphocytes and plasma cells, bacteria, and detritus. The epithelium is irregularly degenerated, owing to the action of the bacteria, but always shows less involvement than would be expected.

·The crypts between the mucous folds form pus pockets. Microscopic abscesses may be seen in the mucosa and *tunica propria*, even extending to the muscularis coat. If healing is to occur and leave an unimpaired tube it must take place at about this stage. If healing does not result the whole process gradually passes on through subacute and chronic stages from which recovery of function is impossible.

The chronic stage, the one almost always seen at necropsy, is dependent upon the continued progress of the infection. Bacteria invade the deeper structures of the tube, producing greater kinking and greater thickening of the walls. Marked changes appear in the mucosa. The epithelial folds, ordinarily quite delicate, become greatly hypertrophied and often adhere to one another. Later actual growth from one to another and across the lumen occurs, and with the gradual distention of the tube they continue to grow, appearing as thin-walled, small, multilocular cavities. The epithelium is yet, for the most part, intact. The exudate gradually subsides and in place of polymorphonuclear leukocytes as seen in the acute stage, the predominating cells seen in the exudate are lymphocytes and plasma cells, with much fibrin. Organization or lysis of the exudate usually begins at this stage. In case of the former the process may progress slowly with gradual diminution of the exudate and progressive organization. The walls become permanently thicker, the mucosa may entirely disappear or the mucous folds, through fibrosis, may become obliterated and thus contribute to the thickening of the wall. Many times this leaves the base of the folds below a solid fibrosed area, as remnants of tubal epithelium. In cross-section these remnants appear as acini of glands. This process may continue to complete stenosis of the duct, with disappearance of the exudate. It often happens that the rate of proliferation and organization is more rapid at one point than another, probably aided by kinking of the tube with stenosis. The favored site for early stenosis is the abdominal osteum with later stenosis at a point below the ampulla. As a result of this stenosis the exudate collects and distends the tube. The adherent mucosa remnants become stretched but are usually sufficiently strong to retain their attachments. The dammed-off portion of the tube in this state of pus distention is known as pyosalpinx (pus tube). It seems that in cattle the distention in salpingitis is never so great as in woman, for rarely are the adherent mucous folds pulled apart or separated and flattened out, but retain the multilocular character. The microörganisms gradually die or are already dead at this time. The pus is gradually absorbed and is replaced by a clear, watery, light straw-colored transudate, or later by mucous secretion from the regenerated tubular epithelium. The fluid contains but few leukocytes. Bacteria may be found present

from the active inflammatory process which preceded, but if careful cultural methods are employed the fluid will usually be found sterile. This last type or stage we designate hydrosalpinx. We are not sure that salpingitis always proceeds as here pictured, but the changes seen indicate previous active infection, for all transitions can be noted between the infective stage and the final. The typical appearance of hydrosalpinx in cattle is a more or less enlarged, thin-walled, tortuous tube, containing a clear fluid. The lumen is marked off by adherent and stretched mucous folds, appearing as small multilocular cysts. Each fold is supported by its basal membrane and lined by quite normal appearing epithelium. It is possible by sufficient distention of the tube to have the flask- or retort-shaped pyosalpinx and hydrosalpinx as seen in women, but we have observed this form only once. One of us has a specimen of this type. Frequently at autopsy only the ampulla will be seen involved. It seems that the uterine end of the tube very often heals but leaves a stenotic ampulla. The ampulla then passes on to chronic salpingitis ending finally in hydrosalpinx and leaving the uterine end of the tube unimpaired. Sometimes the stenosis occurs near the isthmus, in which case the entire tube passes on to chronic salpingitis. The results of salpingitis after the acute stage has passed and the chronic stage begun can always be regarded as producing incurable sterility, in so far as cattle are concerned.

F. Of the SPECIFIC INFECTIONS, tuberculosis and actinomycosis are the only two involving the uterine tubes. Grossly either may appear like a pus tube, or purulent salpingitis, but they are easily differentiated microscopically. Tuberculosis is nearly always secondary to an already existing focus of infection, while actinomycosis is more often primary in the genital organs. In tuberculous salpingitis the tube is swollen and reddened, and pus is found in the lumen. In chronic cases the tubes thicken and become firm and filled with caseous exudate, containing inspissated serum, a few polymorphonuclear leukocytes, plasma cells, and many lymphocytes. Miliary tubercles with or without calcification develop throughout the walls. The reaction involves the mucous folds which become adherent by organization and extension of the tuberculous process and are often entirely replaced by the tubercles and caseation necrosis. In milder cases remnants of epithelium will be seen deep below the newly formed tissue, in this respect appearing often like acini of glands without outlet to the surface. Sometimes in chronic cases the tubes appear beaded through twisting and bulging of the walls, caused by the developing tubercles. The outcome of tuberculous salpingitis may be tuberculous peritonitis, tuberculous metritis, extension to the ovary, generalized miliary infection from invasion of the blood stream, pyosalpinx (pus tube), or a chronic tuberculous salpingitis with-

out healing, but usually with occlusion of the tube. As tuberculosis is usually bilateral, permanent sterility is in most cases an inevitable outcome. Actinomycosis, when developing in the uterine tubes, causes extensive pelvic involvement through extension, by the development of fistulae. It is similar in appearance to actinomycosis elsewhere, and invariably results in permanent sterility of fatal termination.

G. TUBAL GESTATION has been reported in the cow but is so very rarely seen that only passing mention need be made.

DISEASES AND AFFECTIONS OF THE UTERUS

The uterus, of all the genital organs, is the essential one for the development of the embryo. It is often the seat of changes or infections which render the animal temporarily or permanently sterile. The congenital anomalies have been previously mentioned.

A. ACQUIRED ANOMALIES and DEFORMITIES are not commonly seen. They may develop from pelvic and intestinal adhesions following infection, or as the result of tumors of the genital tract or broad ligaments. Torsion of the uterus quite frequently occurs, the cause of which, theoretically, may be similar to those listed for the uterine tubes, but it almost always accompanies gestation. Rupture of the ligamentous attachments of the uterus may render the cow unfit for further pregnancies. Prolapse of the uterus may follow such an accident, but usually results only from dystocia where severe straining and traction are the exciting cause. Lacerations and perforations occur and are usually accidental from obstetrical or surgical manipulation. If peritonitis does not result, these are not ordinarily serious. Loss of cotyledons (carunculae) occurs usually following manual removal of the placenta or following prolapse, but does not as a rule render the animal permanently sterile. It seems rarely to occur.

B. CIRCULATORY DISTURBANCES, such as anemias and hyperemias (acute and passive), are seen. Active hyperemia is physiological in estrum and gestation, and occurs pathologically in inflammations. Passive hyperemias develop as in the uterine tubes. Neither in itself is an important contributory factor to sterility. Anemias may occur as described for the uterine tubes.

C. INFLAMMATIONS are spoken of as metritis, and may conform to the following arbitrary classification, based upon clinical and pathological findings.

    1. Acute metritis—mild or severe
        (a) Puerperal infection
        (b) Non-puerperal infection
    2. Chronic metritis
        (a) Begins as a low-grade infection and continues as such.
        (b) Develops from acute (a or b) by long continued infection.

Some workers further subdivide into acute and chronic endometritis, myometritis, perimetritis, and parametritis. These terms refer simply to location of the inflammatory process, but from the pathological viewpoint can hardly be said to exist as independent disease processes. One type blends closely with the other, so intimate are the anatomical relations. The term metritis will be used in the broad sense with the other terms as descriptive of location.

Etiology.—Metritis in every instance develops as a result of infection. The predisposing causes may be injury, through trauma or irritating fluids, but these only make possible the invasion by bacteria. Eggink (45), in an analysis of 20 cases of acute and chronic metritis, found the following organisms:

B. tuberculosis	2X	Staphylococci	5X
B. pyogenes bovis	14X	B. proteus	3X
Streptococci	12X	B. subtilis	1X
B. coli	6X		

In many of these, mixed infections were present. From analysis of cases the most important organisms appear to be *B. pyogenes,* and streptococci. Except in one case of tuberculous metritis, either or both of these organisms were always found. Lucet (46) first described *B. pyogenes bovis* (1893) when he studied 52 cases of suppuration in cattle. In these he found *B. pyogenes bovis* pure in 10 cases and associated with other bacteria in 7 cases. His type has since been found identical with *B. pyogenes suis* (Grips) and the name *B. pyogenes* has been proposed for both. Künnemann (47) studied many cases of suppuration in cattle and concluded that *B. pyogenes* is the most important etiologic agent. He observed this organism in 90 per cent of cases, in 35 per cent pure and in 55 per cent associated with other organisms. In a survey of 18 cases (purulent, acute, and chronic metritis) reported by Wall (16), the following organisms were found:

B. pyogenes	6X
Streptococci	4X
Streptococci and B. pyogenes	5X
Streptococci and B. coli	1X
Streptococci, B. pyogenes, and B. coli	1X
Streptococci and an anaerobic bacillus	1X

Ward (64) was the first in this country to report on the importance of *Bacillus pyogenes* in animals. Brown and Orcutt (1920) (48) in their "Study of *B. pyogenes,*" worked with 12 strains of the organism, 5 of which were isolated from cases of purulent metritis. The results of the present investigation, which will appear in detail later, confirm the importance of *B. pyogenes* in bovine metritis.

1. Acute metritis of the mild type generally involves the endometrium alone and thus in mild cases acute catarrhal endometritis is frequently seen. It is nearly always the result of an infectious abortion. It may follow retention of afterbirth of full-term gestation, but more often the latter type is more severe. Following the infection of the uterus and placenta by *B. abortus*, an inflammation is set up which results in the premature delivery of the fetus. This organism is not capable of establishing itself in the normal involuted uterus and soon disappears after the abortion. If no secondary infection follows, only a mild acute catarrhal endometritis will ensue, marked by excessive discharge, muco, and muco-purulent, which as involution takes place will rapidly disappear without permanent changes remaining. The superficial lesions seen in the mucous membrane are necrosis and exudative inflammation. The former is a normal accompaniment of involution in the physiologic discharge of the fetal and maternal placenta. Healing in most cases is complete, but Wall (16) states that shrinkage and atrophy of the gland mucosa may occur, with probably similar changes in the carunculae. This change results in no permanent damage to the organ.

2. Acute metritis of the severe type is in the vast majority of cases puerperal in origin (involving endometrium and often other uterine coats). Death and maceration of the fetus *in utero* is frequently a contributing cause, or it follows either infectious abortion or full-time parturition. In either case retained fetal membranes favor the infection, or it may be introduced from the exterior by the operator or accidentally from the vagina. In the majority of non-puerperal infections it follows injury, often during breeding, or through extension of cervical and vaginal infections. The effect of the abortion bacillus on the uterus, in case there is no retention of the placenta, is simply to cause a mild catarrhal endometritis. If the placenta is retained, and this applies to all forms of retention, the involution of the uterus is delayed. Organisms, both parasitic and putrefactive types, enter through the vagina. The mucosa is not able to resist their entrance and severe purulent metritis develops. The mucosa, following delivery, it will be remembered, is deprived for the most part of its epithelium. Carunculae slough off in part, in order to release the fetal chorionic villi. Other cases develop following dystocia, especially when operative procedure is not properly applied, or simply as accidental infections when the utmost care is exercised. The organisms most often associated with this type of infection are streptococci and *Bacillus pyogenes*. Wall (16) makes the observation that if the infection be due purely to streptococci the process heals quite rapidly, but when

resulting from *B. pyogenes,* either pure or associated with other bacteria, pyometra is the rule. The work presented in this paper supports this view.

Pathologic changes.—The endometrium shows necrosis of varying degrees (partly physiological following parturition). It is usually diffuse. Congestion and edema develop coincident with exudative phenomena. At this time large quantities of mucus lie in the cavity of the uterus. Polymorphonuclear leukocytes are seen in great numbers and form a considerable portion of the exudate. The leukocytes gradually increase in numbers until the exudate is decidedly purulent, appearing as thick, creamy pus. As a result of the action of putrefactive bacteria, decomposition of the pus sometimes is noted. *Bacillus proteus,* anaerobic bacilli, and other proteolytic soil types are responsible for the offensive odor. This has nothing to do with the progress of the infection. In the mucosa may be seen large numbers of polymorphonuclear leukocytes, lymphocytes, eosinophiles, and plasma cells, often collected in groups to form microscopic abscesses (not to be mistaken for the normal lymphoid tissue of the uterus which is also accentuated as a result of disease). These even may extend to the muscularis and serosa, but not as a rule. The gland epithelium becomes necrotic and in many cases lost; other glands are blocked in their course by proliferative changes and appear as small cysts. The epithelium of the mucosa generally regenerates but is not of a healthy type, neither is it entirely regenerated during the course of the infection. It is surprising in studying cases of purulent metritis to see the uterus as healthy as it invariably is. The changes in the wall are in no way commensurate with the exudate in the lumen. This type heals early or passes on to the subacute and chronic types.

Symptoms produced are those of general sepsis, as anorexia, slight fever, stupor, and cachexia. As a rule, these symptoms are not marked unless retroperitoneal abscesses develop (localized peritonitis).

Acute metritis may continue to chronic metritis, with development of salpingitis, perimetritis, abscesses of the parametrium (localized peritonitis), ovarian abscesses, or generalized peritonitis with fatal termination. Thrombosis of veins in the vaginal plexus may occur. In other cases it may continue to pyometra as a subacute inflammation, uncomplicated for several weeks, and result in complete recovery when properly treated. Then, too, the condition may have a favorable termination in the incipient stage (especially when of the streptococcus type).

3. Chronic metritis.—In most cases after an acute attack the purulent discharge seems to subside and the observer will think the case healed. This is an expression of closure of the cervical canal. In

many cases, the uterus fails to undergo involution following parturition (subinvolution of the uterus) and throughout the acute attack remains in the evolutionary stage. It gradually fills with the purulent exudate already described, until possibly 5 liters collect. It then begins to ooze from the vagina when the animal is decumbent. This damming up of the exudate we speak of as pyometra. There appears to be in cases of infected uteri, together with the failure of the uterus to undergo involution, also the failure of the *corpus luteum* to disappear (persistent *corpus luteum*), exemplifying the close physiologic relationship existing between the two organs—ovary and uterus. In other cases free drainage is continuous with apparently the same uterine changes, simply a purulent metritis. The course is similar to that already described in acute metritis, and the complications there described are more often delayed until the chronic stages. Recovery in simple purulent metritis without complications, under proper treatment, is often noted. Pathologic changes are similar to those already described for acute metritis, simply more pronounced. The proliferative changes are accentuated, as are also the changes in the gland mucosa. Wall (16) describes regeneration of the normal uterine epithelium by ectodermal types of epithelium as seen in the vagina. This he calls "ectodermoisering." He regards this as a permanent change, affecting the usefulness of the organ. The fibrous tissue is accentuated by proliferative changes, and in the muscularis Wall (16) observed atrophic changes, at other times hypertrophy, depending upon the type of infection. Fibrosis may be so severe that the uterus becomes very hard and thick. In this state the organ is called sclerotic. We have studied and one of us has treated several cases of chronic metritis with excellent results, complete recoveries having occurred.

It is possible that even tho no palpable lesions exist there are physiologic disturbances, producing altered secretion of the glands. The normal uterine secretions, in order to support fertilization of the ova, must be neutral or faintly alkaline. Spermatozoa are killed in acid secretions. Such abnormal secretions are well-known in women and probably give rise to many cases of sterility. If such changes occur in the uterus of the cow no doubt they exert a similar action on the spermatozoa. Since there is a successful treatment for such conditions (alkaline douches) an investigation of this should be continued when material is available.

Hallman (59), in a report on the pathologic findings in eleven cases of bovine sterility, observed alterations of the uterine mucosa varying from slight fibrous thickening of the transverse cervical folds with no apparent alterations of the corporal and cornual mucosa to an atrophic

endometritis. "The lesions observed in varying degrees in the different cases are mucoid degeneration of the superficial epithelium, local and diffuse fibrosis of the uterine mucosae, leukocytic infiltration of the stroma and gland luminae, and degeneration and disintegration of the glandular epithelium with dimunition in the number of glands. In the majority of cases the anatomical alterations are comparatively few and it is hardly conceivable that failure to breed was the result of loss of functional tissue of the uterine mucosa." The studies in the investigation here reported support this view.

4. Chronic catarrhal endometritis is a clinical subdivision of ordinary chronic metritis and the term is used to designate a chronic catarrhal metritis in which there is little formation of purulent exudate. The infection begins usually following abortion or full-term parturition and continues as a low-grade inflammatory process, causing increased secretion and hypertrophy of the mucosa. Cystic and large tortuous glands are often seen. At other times they are atrophic. There is frequently a mucoid degeneration of the mucus secreting glands. From reliable sources the information has been obtained that 90 per cent of the curettements from women, in which curettage has been done for chronic catarrhal endometritis, are normal and that the symptoms observed are the result of altered ovarian function, in most cases, with no evidence of an inflammatory endometrium. It is better to regard these cases, when no active infection can be demonstrated in the endometrium and where pathologic changes exist, not as active inflammations but as the result of acute or chronic metritis, as already described.

D. Hypertrophic endometritis is occasionally seen in the bovine species (60). The uterine mucosa in these cases becomes much thickened. It becomes very vascular and quite susceptible to hemorrhage. The glands enlarge and become cystic and on the surface of the mucosa there develop irregular rounded polypoid-like projections. Many of the cases diagnosed as hypertrophic endometritis, in human practice, have simply been physiological changes of menstruation. There is no doubt, tho, that this type of disease exists. It results in incurable sterility, for in the bovine species curettage is not practiced. The cause is unknown, but by many it is regarded as inflammatory.

E. Cystic degeneration of the uterine walls with hydrometra is described by Williams (60). It is the outcome of many pyometra cases, all severe cases being more or less affected. The uterine glands become cystic, and the uterus may contain much clear fluid. The mucosa grossly appears studded with cysts. Microscopically large, dilated uterine glands are seen. It results from inflammation, a termination of chronic metritis.

F. SPECIFIC INFLAMMATIONS are produced by *B. tuberculosis* and *Actinomyces bovis* and are essentially the same as infections produced elsewhere by these organisms. Sterility with systematic complications usually results, or else these infections are secondary to some more generalized lesions already existing.

G. HEMATOMETRA, distention of the uterine cavity with blood, is rarely seen in the bovine species. Williams (26) describes these cases and states that not infrequently the clot may undergo organization and result in a large uterine hematoma.

H. TUMORS of the uterus, according to Williams (26), are rare. From comparative pathology, leiomyomata should be the most common, with adenomata and carcinomata second. Chorionic epitheliomata and fleshy placental moles have been observed in the bovine species. Tumors, when present, result in sterility, especially when large or growing rapidly.

DISEASES AND AFFECTIONS OF THE CERVIX

As no special attention has been directed toward the consideration of cervical and vaginal diseases which may lead to sterility, only a brief resumé of these will be given in this report.

A. OCCLUSION OF THE OS UTERI, with a cervical canal so tightly closed that spermatozoa can not enter, is rarely found in cows.

B. DILATION OF THE CERVIX UTERI, through loss of muscular tone, is occasionally seen and often the atony is so great that conception can not occur. It is an accompaniment of atony of the uterus in nearly all cases.

C. HYPERTROPHY OF THE EXTERNAL OS UTERI frequently occurs as a result of low-grade proliferative inflammations following injuries at parturition through use of instruments or from extension of vaginal infections. Grossly the folds show great hyperplasia so as partly to block the cervical canal. The mucosa is hyperemic, and often covered with small red papules and vesicles. The epithelium is usually thickened and edematous, while, as a result of rupture of vesicles, it may be desquamated in some places. Sterility is sometimes an accompaniment, but only temporary, until surgical relief can be applied, unless, as is frequently the case, the hypertrophy is occurring with a severe *B. pyogenes* or streptococcus cervicitis and metritis.

D. INFLAMMATIONS OF THE CERVIX AND EXTERNAL OS UTERI often occur as the result of irritating douches, and unless infection supervenes they are only transitory. Infections frequently follow injury at parturition or from use of surgical instruments. They also may develop from extension of metritis and vaginitis, or may be primary at any time. Such infections usually develop slowly with exudation and

proliferation and probably are in most cases caused by streptococci or *Bacillus pyogenes*. The arrangement of the cervical folds in plaits of the mucosa serves to make the infection an obstinate one and difficult to treat. The most frequent complications are hypertrophy of the cervical folds, adhesions resulting in atresia, and extension of the infective process to the uterus and other genital organs. Increased tenacious secretion may result and lead to sterility through mechanically entangling the spermatozoa before they gain entrance to the uterus. This produces a temporary sterility, and in human practice has been found quite amenable to treatment (saline douches). Sterility is present during the infection, but if the infection subsides before pathologic changes are great, judicious treatment usually effects a cure.

E. Tumors such as polypi are reported, but these growths are rare. Malignant carcinomata are not reported as occurring in the cervix of the bovine species.

DISEASES AND AFFECTIONS OF THE VAGINA

A. Congenital abnormalities.—The persistence of the hymen into adult life is occasionally seen and leads to sterility until operative removal. Sometimes a small opening is noted, while in other cases none exists. Bands are sometimes seen representing the embryonic median walls of the fused Müllerian ducts, which have failed to atrophy and disappear completely. They may persist so completely as to constitute essentially a double vagina (Williams (26)). They can, as a rule, be reduced by surgical procedure so that permanent sterility is not a result. The almost complete absence of vagina in freemartins and other anomalies and arrests in development of the genital tract have been mentioned.

B. Acquired anomalies and defects.—Between the walls of the vagina, as the result of proliferative changes following infections, strong connective tissue bands frequently develop resulting in atresia of the vaginal walls. One such case is included in the case reports which follow. The stricture, when extensive, renders the animal sterile; when slight, surgical interference usually results in recovery.

C. Hypertrophy of the vaginal walls.—This is frequently seen, occurring during the late stages of gestation and in the nonpregnant animal. The wall of the vagina, 10 to 12 cm. anterior to the vulva, laterally and dorsally becomes hyperplastic so that partial prolapse of the vagina results, ordinarily seen only while the animal is decumbent. Severe inflammatory changes sometimes develop and result in more complete prolapse, induced by straining from the irritation. The condition is ordinarily successfully treated through surgical removal of the hyperplastic portion of the wall.

D. PROLAPSE OF THE VAGINA is seen in cases other than from the development of hypertrophic walls. It is occasioned by late pregnancy, especially in fleshy animals, and from injuries following parturition. The prolapse is frequently not complete, and is visible only while the animal is decumbent, but may be severe and complete.

E. VAGINISMUS (violent spasms of the vagina) is a frequent symptom of disease of the genital tract and ovaries. These spasms influence conception and may be relieved when the cause is removed. Their influence on conception in the animal is only secondary.

F. CYSTS OF GÄRTNER'S DUCTS (remnants of the Wolffian duct) may interfere with successful breeding but do not result in absolute sterility.

G. CYSTS OF BARTHOLIN'S DUCT are described by Hess (49) and Hofman (50). The glands and ducts become hyperplastic and cystic. Until surgically removed they may prevent conception.

H. INFLAMMATIONS in most cases are the result of infections. Injuries or irritating chemicals may influence their development. Two types of inflammatory changes are seen:

    1. Granular venereal disease.

    2. Non-specific purulent inflammations.

1. Granular venereal disease is an infectious vaginal disease, occurring very commonly in cows (according to Williams in 86 per cent of cows examined). It is characterized by the development of hard, yellowish granular nodules on the edematous vaginal mucosa. The etiologic agent has not been definitely determined but most workers favor the streptococcus as the cause. Williams (51) called attention to the prevalence of the condition and its possible relationship to infectious abortion, but *B. abortus* probably has no relation to the condition. Pathologic changes are hyperemia and edema of the vaginal mucosa, with the formation of tiny granular yellowish vesicles. Increased catarrhal exudate is an accompaniment. The vesicles are an enlargement of the lymph follicles, which, owing to the inflammation, are edematous, swollen and hyperemic. The disease probably has no relation to sterility, except that through its presence saprophytic bacteria of the lactic acid type enter and render the secretions acid, thus inhibiting the penetration of living spermatozoa into the uterus. Other saprophytic types may through enzymic action so attenuate or kill the spermatozoa that fertilization of the ova is impossible.

2. Nonspecific purulent inflammations occur principally following parturition. They are of comparatively infrequent occurrence. The majority of cases seen and diagnosed vaginitis clinically, are simply drainage of pus from the uterus and cervix without inflammatory reaction in the vagina. The vagina, because of its stratified epithelial

surface, is not prone to become infected unless already mechanically injured any more than is the external surface of the body. No study has been made of vaginitis but probably *B. coli* and staphylococci are more often the etiologic agents than are streptococci or *B. pyogenes*. The pathologic changes are similar to those seen on any mucous membrane, and are in most cases only acute, accompanied by a mucopurulent discharge.

I. TUMORS, such as polypoid masses and papillomata, are sometimes seen but are not common. Carcinomata and sarcomata are rarely seen in this location, in the bovine species. Williams states that carcinoma of the vulva is not rare in the cow.

J. DISEASES OF THE PELVIC BONES, altho rarely seen, are productive of sterility in that the animal can no longer carry the fetus properly. Fracture of the ileum through injury may be responsible for this condition. Osteomalacia may render the pelvic bones friable and result in narrowing of the pelvic inlet to such an extent that parturition is difficult or impossible. So-called dropping of the tail head (sacrum) may produce a similar result. In nymphomania (cystic ovaries) the tail head often becomes raised through relaxation of the pelvic ligaments. Misplaced genitals may result, but are returned to normal when the cause (cystic ovaries) is removed.

THE PRESENT INVESTIGATION

METHODS OF STUDY

The object in view during the progress of this investigation has been to obtain cases which were diagnosed by clinical procedure as sterile. Sterility in some instances was considered as absolute, and cases falling into this group were slaughtered and the genital organs studied both pathologically and bacteriologically. Clinical history, altho not always complete, is available in all cases of this group. Other animals were presented at the University clinic for treatment of sterility, the majority of which responded favorably to the clinical procedure employed. Improvement in this group was apparent, with suggestion of recovery. Since the affected animals were valuable purebred stock, slaughter was not advised. In these cases bacteriological studies combined with clinical data constitute the report. When possible, cultures were obtained from the genital tract (uterus) during the progress of the infection by inserting sterile swabs through the cervical canal into the uterus. The same method was employed in all cases where the genital tract was cultured during the life of the animal. At necropsy the genital organs were carefully removed, and systematically cultured. The organs were seared at the point of study

and penetrated with sterile instruments. At the point of penetration, material for cultural study was obtained. Cultures were prepared on 10 per cent sterile horse serum agar and the tubes sealed with hot wax. These were allowed to incubate from 10 to 14 days at 37°C. By this method types such as *Bact. abortus* could develop. The aerobic cultures were prepared by the plate method, using agar in combination with sterile defibrinated horse blood. By this method streptococci and *B. pyogenes* were most easily obtained in pure culture. As soon as possible after cultures were prepared, sections were taken from various parts of the genital tract. Preservation and fixation were accomplished in Zenker's solution, and in 10 per cent formalin. Sections were cut by the paraffin method, and also by the freezing method. Hematoxylin and eosin were employed in the staining technique. Cultures were identified individually. In all instances the most modern and also original references were consulted. For *Bacillus pyogenes* the original work of Lucet (46), Künnemann (47), Grips (52), Glage (53), and Brown (48) were consulted. For the work on streptococci, the works of Brown (56) and Hollman (55) have been used exclusively. The work of Winslow (54) et al. has been followed in studies on the staphylococci. In all, nineteen cases are reported, only one without clinical history, this being a case of tuberculous metritis and salpingitis obtained at the abattoir.

CASE REPORTS

CASE I

Clinical history.—Jersey cow, 5 years old. First calf born at two and one half years of age, full term but born dead. Agglutination reaction for infectious abortion, positive up to 1-200, May, 1918. Second calf aborted June, 1918. Received into University experimental herd December, 1918. Bred January 27, 1919; examined and pronounced pregnant March 6; examined again in April, at which time found non-pregnant. It is assumed as reasonably certain that she aborted between first and second examinations for pregnancy. Bred April 14, May 25, and June 24, 1919. The animal never showed any extreme signs of heat, coming in and going out normally. Bred again July 5 and July 29, 1919. Allowed to rest for several months. Uterus examined and massaged without detecting any abnormality. Bred October 18, 1919, November 28, 1919, January 22, 1920, and February 5, 1920. Examined again March 15, 1920, and found to be non-pregnant, genital organs apparently normal. Agglutination reactions of blood to *B. abortus* antigen, after the animal entered the University herd were as follows: November, 1919, and March, 1920, positive 1-20 to 1-1000 and inclusive dilutions. The history of the

animal indicates the prevalence of sterility in the herd from which she came. The mother was difficult to get with calf, but never aborted. After parturition there was usually retention of the placenta. One sister of cow, case 1, was sold for beef because of sterility, and another was recently sent to our experimental herd because of frequent abortions (last three calves aborted). The animal's condition (case 1) was considered incurable, and she was slaughtered March 30, 1920.

Necropsy

1. *Gross description.*—The general condition of the carcass is good. The vagina is normal. The cervix is normal. The uterus appears normal. The *tubae uterinae* appear normal. The right ovary is 3 cm. in length, and 2 cm. in width. It appears to be more adherent than normal to the broad ligament. It contains a *corpus luteum* 8 mm. in diameter. The left ovary is 2.7 mm. long, 1.3 mm. wide. It contains a persistent *corpus luteum* deeply buried in its stroma. The *corpus luteum* is 2.5 cm. in diameter. The center of the *corpus luteum* presents a cystic cavity 1 cm. in diameter. The ovarian tissue is greatly flattened over this retained and cystic *corpus luteum.*

2. *Microscopical description.*—The vagina and *cervix uteri* are normal. In the uterus some of the innermost glands show degenerative changes. The glands are enlarged, and the epithelium of many is partly degenerated. In the lumina there is an exudate containing desquamated cells and mucus. The nuclei of the gland cells are pyknotic. All the deeper lying glands are normal. The stroma of the gland mucosa is less cellular than normal, owing to increased connective tissue proliferation, mostly collagenous fibrils. The other coats of the organ are normal. The uterine tubes are normal. There are many primitive follicles in the cortex of the right ovary. Lying deeper in the ovarian cortex there are three follicles (in one portion of the ovary), showing atretic degeneration. The *theca folliculi* of these follicles is greatly thickened, and is very cellular. The *membrana granulosa* of the smaller follicles is so proliferated as almost completely to fill the central cavity. In the larger ones these cells are increased in number, many of them being detached from their normal attachment and lying free in the central cavity. Many of these cells have pyknotic nuclei and their cytoplasm shows a hyaline granular degeneration. Figure 1 illustrates this condition. *Corpora albicantia* are numerous throughout the ovarian stroma. Several normal, nearly mature, Graafian follicles are present. Other sections appear normal.

3. *Bacteriological findings.*—

    1. Cultures from the uterus, uterine tubes, and ovaries remained sterile.

    2. Three types of organisms developed from the vagina:

    (a) *Staphylococcus aureus* (Rosenbach); (b), *B. coli communis;*

    (c) *B. subtilis*

4. *Diagnosis and discussion.*—The etiology of sterility in this case is not clear. Possibly the deep seated cystic *corpus luteum* which was present in the left ovary was a contributing factor. The degenerative changes described in follicles in the right ovary may also have influenced the progress of the condition. The changes in the uterine glands may also have been sufficiently pronounced to inhibit implantation of the developing embryo, or to inhibit passage of spermatozoa to the ovum. The most probable change responsible for sterility is that described for the ovaries.

CASE 2

Clinical history.—Shorthorn heifer. Bred for first time April 3, 1920. Appeared in estrum again April 26, and was rebred to same sire. Immediately after this service the heifer was noticed to be suffering considerable pain. At termination of next diestrum, heat did not appear, but pregnancy was not suspected on account of a fairly copious and constant vaginal discharge. The discharge was of a mucopurulent nature, yellowish gray in color, and had a pronounced offensive odor. The discharge also at times was streaked with blood. A physical examination of the vagina revealed severe tho not active inflammatory changes. The mucous membrane of the vagina was studded with small vesicles, such as characterize granular venereal disease. Cervicitis was pronounced. The *os uteri externum* was covered by a profuse mucopurulent exudate. The cervical canal was partially obstructed by inflammatory changes. A rectal examination was made with considerable difficulty owing to formation of massive adhesions between the uterus, ovaries, and walls of the rectum and colon. This resulted in constriction of the lumen of this portion of the intestinal tract. The right ovary was found to be enlarged and adherent to the right uterine horn. The right uterine tube was sufficiently distended to render it easy to locate and was adherent to the ovary. The left ovary contained a large cyst. It was enlarged and irregular in outline and adherent to the left uterine horn. The left uterine tube was not definitely located. The body and horns of the uterus were difficult to palpate, but were thought to be somewhat hard and thickened. A diagnosis of incurable sterility was made and the animal was slaughtered for food.

Necropsy

1. *Gross description.*—The physical condition of the carcass is good. The vaginal mucosa appears practically normal. The *corpus uteri* is indurated, and adherent by fibrous attachments to the rectum. No macroscopic changes are apparent in the endometrium. The *cervix uteri* is inflamed and the cervical canal is more or less obliterated and tightly contracted. The *cornua uteri* appear normal in the gross structure. In the lumen of the uterus, throughout its entire length, a considerable mucopurulent discharge is present. Some areas show pus undergoing caseation without marked foul odor. The uterine tubes are dilated to 6 mm. throughout their entire length. The walls are thick and fibrous. At the isthmus the dilation forms a definite pus pocket, being 2 cm. in diameter and extending upward on the tube 3 cm. The fimbriated ends are adherent to the broad ligament. In the lumen there appears a mucopurulent exudate. This purulent material is odorless. The left ovary is firmly adherent to the uterus by fibrous attachments which extend from the body to the horn. It averages 6-8 cm. in diameter. The capsule is slightly thickened. On its inner border there is a large, persistent *corpus luteum*. The central portion of the ovary is cystic. The cyst measures approximately 4 by 5 cm. in diameter. The right ovary is very irregular in outline, and is comparable in size to the left. A sagittal section shows only a small amount of normal ovarian tissue. Centrally located and surrounded by ovarian tissue is an abscess, the content of which is greenish yellow and pasty in consistency. The pus is putrid, having a stale, pungent odor. The ovarian tissue forms a wall 1¼ cm. thick around the abscess. At the inner periphery and separated from the abscess by a slight constriction and wall of connective tissue, is a small cyst containing a straw-colored serous fluid. The cyst is 1 cm. in diameter, oval in shape, and enveloped by a hard but thin fibrous wall.

2. *Microscopical description.*—The endometrium of the uterus shows a partially exfoliated epithelium, only shreds remaining in which the nuclei are barely visible. That which remains intact is normal except for the frequent presence of leukocytes, and is composed of a simple columnar epithelium. Many uterine glands are cystic. The cysts are three or more diameters larger than the normal glands and are made up of an outer wall composed of dense connective tissue fibers. These support, in a few places, a single layer of epithelial cells of low columnar type. Degeneration of this epithelium is pronounced. In the cystic cavity very little cellular material appears, only a few polymorphonuclear leukocytes and mononuclear leukocytes and a small amount of fibrin can be seen. Similar inflammatory cells

extend into the cystic wall. Uterine glands in the vicinity of those which are cystic show atrophy, due to an overgrowth of connective tissue. This also appears in other areas where no cysts are seen. The epithelium of many glands is entirely atrophied and replaced by proliferations of young connective tissue cells. The stroma in general shows a high degree of inflammatory reaction, there being quite universally present, polymorphonuclear leukocytes, lymphocytes, plasplasma cells, and fibroblasts. In some areas these are collected so as to form small abscesses. The myometrium shows similar but less extensive cellular infiltration. The serosa is normal. The uterine tubes show a normal serosa. The muscular coat is atrophied at the expense of connective tissue proliferations. The epithelium of the mucosa is simple columnar, and is exfoliated in some areas. Where exfoliation appears the cells are degenerated and only a homogenous, eosin-staining, fibrin-like material remains. In the *tunica propria,* there are masses of polymorphonuclear leukocytes closely packed so as to form small abscesses in the wall. The lumen contains dense masses of leukocytes, mostly polymorphonuclear, and small mononuclear cells, among which plasma cells are occasionally seen. Some fibrin is also present. Necrosis of the inflammatory elements has commenced in the central portion. The medulla of the right ovary consists for the most part of fibrous connective tissue. Several areas show collections of leukocytes, mostly polymorphonuclear and mononuclear cells. In some places these form small abscesses. In the cortex the stroma is very vascular. In one section there appears an atretic follicle. One section shows a cystic follicle, with the *theca folliculi* greatly thickened. Only remnants of the *stratum granulosum* remain. Many of the nuclei of this layer are pyknotic.

3. *Bacteriological findings.*—

(1) Uterus and uterine tubes

    (a) *Staphylococcus epidermidis* (Gordon)

    (b) *B. coli communis*

    (c) *B. pyogenes* (Lucet)

    (d) *Streptococcus mitis* (Alpha type)

(2) Right ovarian abscess

    (a) *Staphylococcus aureus* (Rosenbach)

    (b) *Streptococcus mitis*

3. Right ovarian cyst   (a) Sterile.

4. *Diagnosis and discussion.*—1. Purulent cervicitis, metritis, and salpingitis. 2. The uterus shows evidence of chronic changes, such as fibrosis and cystic glands in the endometrium. 3. Right ovarian abscess, with chronic inflammation of right ovary. 4. Small follicles

showing cystic and atretic degeneration are also seen. 5. *Corpus luteum* cyst of left ovary. These changes support the diagnosis of incurable sterility. Infection most likely entered through injury at time of breeding and gradually proceeded to involve the entire genital tract.

CASE 3

Clinical history.—Beauty Frances, Holstein cow, 2 years old, delivered a dead full-term calf following severe dystocia on September 23, 1920. Traction necessary to make delivery. Placenta came away normally. Developed severe purulent metritis within five days after parturition. Parauterine abscesses soon developed, the larger of these being located on the superior surface of the vagina between the left side of the uterus and the rectum, in the pelvic cavity. This measured approximately 8 inches in length by 4 in width. Small abscesses over the external wall of the uterus could be palpated, the size of which varied from that of a pea to that of a walnut. The ovaries were also enlarged and thought by rectal palpation to contain abscesses. The large abscess was evacuated on October 13, 1921. From this ½ liter of thick creamy pus streaked with blood was obtained. On October 23, 1921, the abscess was again evacuated. The pus this time was similar, but brown in color and had an offensive odor. Cultures were prepared from the purulent exudate, from which the following organisms were isolated: (a) *B. pyogenes* (Lucet), (b) *Streptococcus anginosus* (Beta type). At this examination another abscess over the left horn and extending to the ovary was palpated. This was not opened. The animal became emaciated, showed slight intermittent fever, and loss of appetite. The lesions became progressively worse and slaughter was advised on December 17, 1920.

Necropsy

1. *Gross description.*—The cervix and *corpus uteri* are drawn downward to the left owing to the adhesions and weight of the abscesses. The cervix appears normal. The body of the uterus is 3 cm. in length and its mucosa appears normal. The right uterine horn and right ovary are drawn downward and backward. An abscess is present on the right horn, 9 cm. anterior to the *corpus uteri*. This involves the perimetrium. The abscess is 3 cm. in diameter. The right horn is adherent in many places to the rectum and colon. The carunculae are dull white in color. They measure from 1 to 15 mm. across the surface and rise to a height of from 3 to 5 mm. from the gland mucosa. The gland mucosa is inflamed. There is no accumulation of pus in this horn. The left uterine horn proceeds forward and outward over a large abscess, to which it is firmly adherent. It

turns abruptly at a distance of 10 cm. anterior to the body of the uterus, the turn forming an angle of 45 degrees. Very few carunculae appear in the first portion of the horn. They become more numerous in the anterior half. Below the horn and adherent to it is a large abscess which measures 14 cm. in length and 10 cm. in width. Smaller secondary abscesses are present on the surface of the larger one. The abscess wall is thick and fibrous and its contents are thick, pasty, and malodorous. The abscess is adherent to the pelvic wall and colon. The right *tuba uterina* is normal. The left *tuba uterina* enters the large abscess at a distance of 4 cm. from the tip of the horn. As it enters the abscess it is lost to view. The right ovary measures 4 cm. in length, 3 cm. in width, and 2 cm. in depth. It contains a *corpus luteum* measuring 2.5 cm. in diameter. The center is cystic. Ventral to the *corpus luteum*, in the ovarian stroma, there is a cyst, measuring 17 mm. in diameter. Many Graafian follicles appear on the surface of the organ. The left ovary is buried in the large abscess from which it can not be differentiated.

2. *Microscopical description.*—The cervix appears normal. The uterus shows a quite uniform degeneration of uterine glands. This change is especially marked in the glands nearer the lumen of the organ. The epithelium of the glands shows granular degeneration of the cytoplasm, with only remnants of cells remaining. The nuclei are markedly pyknotic. Some show a marked infiltration with lymphocytes. The epithelium of the mucosa is in most places desquamated. In the lumen of the organ is occasionally seen an exudate, consisting of inspissated serum, lymphocytes, and large mononuclear cells. There is an increased activity on the part of the mucosa of the right uterine tube. Considerable mucus appears in the lumen, together with marked losses of epithelium. A few lymphocytes appear in the lumen which also infiltrate the mucosa. The right ovary presents many Graafian follicles which show marked cystic changes. These range in size from very small follicles to those measuring from 2 to 3 mm. in diameter. The nuclei of cells of the *membrana granulosa* are markedly pyknotic. The *liquor folliculi* instead of being very light, is precipitated as dense, homogenous, deep eosin-staining material. An example of this is illustrated in Figure 3. Sections of the wall of the large cyst show it to be of an edematous, thick, supporting, connective tissue structure. The *theca folliculi* and *membrana granulosa* are flattened out through great distention of the follicle. The primitive follicles appear normal. In one section there is also present a small *corpus luteum* cyst. This is approximately 1 mm. in diameter. The central portion is composed of a deep eosin-staining, homogenous, coagulated

fluid. The inner border is composed of lutein cells supported by connective tissue and remains of the *theca folliculi*. *Corpora albicantia* are numerous throughout the ovarian cortex. Sections of the wall of the large abscess show the wall to be composed externally of dense collagen fibrils. Toward the inner wall the connective tissue becomes more fibrillar. This shows quite a uniform infiltration with polymorphonuclear leukocytes, large mononuclear leukocytes, and plasma cells. The inner portion is almost entirely composed of exudative cellular material supported by young connective tissue fibers.

3. *Bacteriological findings.*—
    (1) Body of uterus, sterile
    (2) Right *cornu uteri, B. pyogenes* (Lucet)
    (3) Left *cornu uteri,* sterile
    (4) Right uterine tube, sterile
    (5) Right ovary, sterile
    (6) Abscesses   (a) *B. pyogenes* (Lucet)
                   (b) *Streptococcus anginosus* (Beta type).

4. *Diagnosis and discussion.*—
    1. Mild chronic metritis
    2. Catarrhal inflammation of right uterine tube
    3. Cystic degeneration of Graafian follicles and small *corpus luteum* cyst in right ovary
    4. Periuterine and parauterine abscesses, with abscess formation about the left uterine tube and left ovary.

The persistence of infection about the uterus without involvement of that organ to any marked extent, is remarkable. The presence of large periuterine abscesses would undoubtedly lead to permanent sterility through adhesions, even tho the genital organs themselves remain comparatively free from infection. The changes in the Graafian follicles may be the result of inflammation or disturbed uterine function. This is not known.

CASE 4

Clinical history.—Pauline, Holstein cow, 2 years old. Last pregnancy terminated September 6, 1920, with a premature delivery of the fetus. The fetus was coated with a yellowish brown, semi-turbid, tenacious exudate. The placenta was retained and removed 24 hours following parturition. Rectal examination and palpation of genital organs on October 23 revealed a large abscess, the size of an orange, in the left ovary. This was evacuated through the vagina. The cow suffered considerable shock following the operation and lactation became diminished for a number of hours. Had symptoms of severe abdominal pains, and loss of appetite for twelve hours. Gradually returned to normal. Examined on November 2, the abscess had again

enlarged with marked adhesions between left ovary and uterine horns. The abscess became larger very rapidly, with development of marked adhesions throughout the pelvis. Animal was regarded as incurably sterile and owner was advised to slaughter. Cultural studies of the purulent exudate were made from time to time. The bacterial flora consisted of (a) *B. pyogenes* (Lucet), (b) *Staphylococcus candidus* (Cohn), and (c) *Streptococcus fecalis* (Alpha type). The animal was slaughtered on December 7, 1920.

Necropsy

1. *Gross description.*—Carcass is poorly nourished. There is an abscess 28 by 23 cm. situated in the left pelvic cavity. This is adherent to adjacent muscles, broad ligament, uterus, left ovary, intestines, and peritoneum. It is well encapsulated and easily separated from its attachments. The walls are thick, and within them is a large quantity of pus. The pus is partly caseous and partly liquified. The odor is extremely offensive. The vagina is normal. The cervical canal of the uterus also appears normal. The right *cornua uteri* runs in a normal direction forward, downward, and outward, and the tip of the horn is curved backward to the *corpus uteri*, where the ovary is attached. The right horn and the body of the uterus contain no pus. The carunculae are very prominent. The tips are deeply congested, and measure 13 by 8 mm. across the surface. They rise from the gland mucosa, on the average, 4 mm. The left uterine horn proceeds in an irregular manner forward and outward. It then turns upward and again downward, over a large parauterine abscess. It coils itself about this abscess and adheres closely to it. The tip of the cornua is pressed between the two abscesses and is lost to view in the inflammatory overgrowths. There is no pus in the lumen. The carunculae are large and appear inflamed. They average in size, across their flattened surface, 6 by 12 mm. and extend upward from the surrounding mucosa from 2 to 3 mm. The right *tuba uterina* is normal in appearance. The left is not visible because of extensive abscess formation about it. The right ovary appears normal. It measures 3 cm. in length, 1.5 cm. in width, and 1 cm. in depth. The left ovary is buried in the abscesses which have formed about it so that it is completely lost to view. The abscesses on the left horn, not included in the parauterine abscesses previously described, are two in number. One lies beneath the horn and the other anterior to it. The former is 12 by 15 cm. in size, and the latter 6 by 8 cm. These abscesses and both horns are adherent to the pelvic walls, colon, and rectum.

2. *Microscopical description.*—The cervix is normal. The mucosa of the uterus is in the resting stage. The glands, for the most part, are very small. There appears to be in some areas an overgrowth

of connective tissue, and in other areas the walls are edematous. There is an increase of lymphocytes, mononuclear leukocytes, and plasma cells in the stroma of the gland mucosa. In the acini of some of the glands, lymphocytes are present. A few peripheral glands show degeneration of the epithelium. The right uterine tube is practically normal. In the right ovary there are many degenerating Graafian follicles. The cells of the *membrana granulosa* are partly degenerated, the nuclei of which show pyknosis and karyorrhexis. The *liquor folliculi* is replaced by a more heavily precipitated fluid. It appears homogenous and is deeply stained with eosin. In some follicles where ova appear, the cells of the *cumulus oöphorus* are degenerated similar to those of the *membrana granulosa*. In the ovum the cytoplasm appears to have undergone a hyaline degenerative change. Other areas show small cysts lined by lutein cells. These are small cystic remains of *corpora lutea. Corpora albicantia* are numerous.

3. *Bacteriological findings.—*
     (1) *Corpus uteri,* sterile
     (2) *Cornua uteri,* sterile
     (3) Right uterine tube, sterile
     (4) Right ovary, sterile
     (5) Parauterine abscess   (a) *B. pyogenes*
                           (b) *Streptococcus fecalis* (Alpha type)
                           (c) *B. proteus*
                           (d) *Staphylococcus candidus* (Cohn)
     (6) Periuterine abscesses, same except no *B. proteus* isolated.
4. *Diagnosis and discussion.—*
     (1) Mild non-purulent metritis
     (2) Cystic degeneration of Graafian follicles of right ovary
     (3) Periuterine and parauterine abscesses

The absence of bacteria in the genital organs cultured is comparable to the results obtained in case 3. The infective process seems to be completely localized with ability of the mucosa of the genital tract to withstand the invasion of the organisms. This immunity from attack, no doubt, would not be permanent, for sooner or later the progress of the infection would lead to definite changes in the uterus and right uterine tube, such as have already occurred in the left uterine tube and left ovary. The cystic degeneration of medium sized Graafian follicles, whether of importance or not, is at least an interesting observation.

CASE 5

Clinical history.—Aged Holstein cow, Lady Astrea. Calved normally in 1919, aborted April 15, 1920. Retained placenta was followed by a severe metritis. She was three months recovering from this. No treatment was administered after the placenta was removed. Examined October 13, 1920, and pronounced incurably sterile. Slaughtered October 29, 1920.

Necropsy

1. *Gross description.*—The carcass is well nourished. The cervical canal is tightly closed, but does not appear inflamed. The body of the uterus and horns is thickened. The mucosa of the uterus is not inflamed. The carunculae are normal. The right uterine tube is adherent to the right horn of the uterus. The uterine tube is enlarged, especially pronounced at the fimbriated end, and near the uterine end it appears normal. The tube is very tortuous at the fimbriated end. It is dilated to 1 cm. in diameter, and contains a clear straw-colored fluid. The lumen is crossed by interlacing bands, giving it a multi-locular appearance. The tube winds its course through a mass of connective tissue, which in some places is so dense that it can not be definitely seen. Near the uterine end the tube is 2 mm. in diameter. At the fimbriated extremity, there appears an abscess, adherent to the uterine tube and right ovary. It measures 2 cm. in diameter, and is completely encapsulated within a thin wall. The pus it contains is not malodorous, is pasty in consistency, and greenish yellow in color. The left ovary is 4 cm. in length and 2.5 cm. in width. On the surface there are many small follicles, and buried in the substance of the ovary, there is a large *corpus luteum.* It is 1.5 cm. in diameter at the surface of the ovary and extends into its substance 13 mm. The right ovary is approximately 3.5 cm. in length and 2.5 cm. in width. It is encapsulated by a firm connective tissue capsule. The ovary is very hard and the cut surface shows no visible ripe follicles, except at one border, where a small portion of normal appearing ovarian tissue is seen. The intestines and mesentery are firmly adherent to the right ovary.

2. *Microscopical description.*—The cervix is normal. The uterus is normal. The uterine mucosa is in the resting stage, as shown by the small inactive glands. The left *tuba uterina* is normal. The right *tuba uterina* is normal at the isthmus. Sections across the tube near the ampulla show a tube with a greatly thickened wall, due to proliferation of the connective tissue. There is also fibrous thickening of the mucous folds. This has formed adhesions between the folds, leaving gland-like structures enclosed within masses of connective tissue. These structures are lined with a low cuboidal epithelium

and contain precipitate of serous fluid and mucin. Some have become greatly dilated by the retained fluid. In the center the fibrosis has been so complete that the attachments extend across the lumen and connect with similar areas on the opposite side. Some of the mucous folds do not appear to have undergone much thickening, but in places are elongated and flattened out. Throughout the areas of fibrosis, and in the lumen of the dilated structures, there are lymphocytes and occasionally polymorphonuclear leukocytes. The inflammatory cells are, however, not numerous. The left ovary shows many small cystic Graafian follicles. The *membrana granulosa* is mostly degenerated, and the *liquor folliculi* is replaced by a thick, dark-staining, homogeneous material. Some of the follicles show another type of degeneration, as pictured in Figures 1 and 2. These show a greatly thickened *theca folliculi* and proliferated epithelial cells of the *membrana granulosa* and may be interpreted as atretic follicles. Some sections show small cystic *corpora lutea*. Surrounding the wall is seen connective tissue, lying within which is an area resembling the *corpus albicans*. The innermost portion of the wall is composed of a thin layer of lutein cells. The content of the cyst is not rich in albumin or mucin, for the precipitate is light and granular. The right ovary shows similar cystic changes of the Graafian follicles. The most evident lesion, however, is the marked increase of connective tissue, leaving a sclerotic organ. Sections through the abscess show a dense capsule of connective tissue. Toward the innermost portions the cells of the exudate are closely packed. Polymorphonuclear leukocytes predominate, with plasma cells and large clear mononuclear leukocytes rather numerous.

3. *Bacteriological findings.—*

    (1) *Corpus uteri,* sterile

    (2) Right *cornu uteri, B. pyogenes* (Lucet)

    (3) Right *tuba uterina*   (a) *Staphylococcus candidus* (Cohn)

                          (b) *Streptococcus ignavus* (Alpha type)

                          (c) *B. pyogenes* (Lucet)

    (4) Right ovary, sterile. Cyst, *B. pyogenes*

    (5) Left *cornu uteri,* sterile

    (6) Left *tuba uterina,* sterile

    (7) Left ovary, sterile

    (8) Tubal abscess   (a) *B. pyogenes* (Lucet)

                         (b) *Streptococcus ignavus*

4. *Diagnosis and discussion.*—

(1) Hydrosalpinx of right *tuba uterina*

(2) Abscess of fimbria of right *tuba uterina*

(3) Sclerosis of right ovary, with cystic degeneration of many Graafian follicles

(4) Cystic degeneration of Graafian follicles of left ovary

The fact that sterility existed in this case with only obstruction of the uterine tube on the right side indicates the close relationship between ovary and sterility. Evidently the ova in the left ovary were degenerated when set free, or the pathologic condition of the right side prevented fertilization and implantation of the ova from the left ovary.

CASE 6

Clinical history.—Holstein cow, 12 years old. Calved normally December 7, 1919. Bred January 20, 1920; April 7, 1920; July 17, 1920. No history of disease. Examined October 13, 1920. The examination showed hydrosalpinx in both uterine tubes, and both ovaries large and cystic. The animal was pronounced incurably sterile and slaughtered October 29, 1920.

Necropsy

1. *Gross description.*—The carcass is well nourished. The cervix is partially dilated. It appears normal in structure except for small cysts which appear deep in the structure of the internal *os uteri.* A small tumor projects from the outer surface of the body of the uterus. It is 2 cm. in diameter and is located in the muscular coat of the uterus, and gives the rounded prominence seen on the serosa of the *corpus uteri.* The growth is soft, circumscribed, and pink in color. The mucosa of the uterus appears normal. The right uterine tube begins as a normal structure. It gradually enlarges until it reaches a diameter of 1.5 cm. The tube is hard, and runs a markedly tortuous course. It contains a thin straw-colored fluid in its lumen. The lumen is for the most part obliterated and replaced by interlacing strands of tissue giving it a multilocular appearance. At the fimbria the tube is adherent to the right ovary. The left uterine tube presents the same picture as the right, except that it is smaller and not adherent to the ovary at the fimbriated extremity. The right ovary is 3 cm. in length and 2 cm. in width. It is hard and fibrous in appearance, and is covered by a firm, hard capsule. In the center of the ovary there is a large persistent *corpus luteum.* It measures 1.5 cm. in diameter. The outer wall is yellow in color (2 mm. thick), and the center presents a hard dark red mass which is not adherent to the lutein tissue of the wall. The central mass is from 0.5 to 1 cm. in

diameter. The left ovary is comparable in size to the right one. It contains a *corpus luteum* and appears normal.

2. *Microscopic description.*—The cervix shows a normal mucosa. The internal portion adjacent to the *corpus uteri* has many cystic glands deep in its wall, surrounded by the myometrium. The largest of the glands is 1.5 cm. in length and 1.5 cm. in width. The cystic glands are lined by simple cuboidal epithelium, and the outline is very irregular. The precipitated content of these cysts is in most instances very small in amount, but in one it is dense, homogenous, and eosin-staining. The epithelium of the uterine mucosa, in some places, appears thicker than normal. This is evident both in the cornua and in the *corpus uteri*. The epithelial cells are flat instead of columnar, in these areas, and are several layers in thickness instead of simple. Adjacent to these apparently squamous cell and thickened epithelial areas, the cells are simple columnar in type. This may be interpreted as "ectodermoisering," described by Wall. The uterus appears normal in every other respect. Sections through the tumor, described in the wall of the *corpus uteri,* show it to be composed of smooth muscle, well circumscribed by connective tissue. The gland mucosa is in a resting state. Sections through the enlarged *tubae uterinae* show a comparatively thin wall, consisting almost entirely of connective tissue. The mucous membrane consists of a greatly flattened simple cuboidal epithelium. The folds of the mucosa are stretched and converge toward the center where the connective tissue is much more pronounced, giving the central convergent folds great thickness. In this, collapsed adherent folds are completely surrounded by edematous connective tissue and appear as acini of glands. The adherent folds give the tube an appearance of multilocular cysts, all lined by the same type of low epithelium. They contain a faintly hematoxylin staining material indicating its mucinous composition. Inflammatory cells are not numerous and when present consist of lymphocytes. The ovaries are sclerotic. Primitive Graafian follicles are very few in number, and *corpora albicantia* are very numerous. A few Graafian follicles show degenerative changes characterized by flattening and stretching of the *membrana granulosa* to a single layer of cells and replacement of the *liquor folliculi* by a more dense material having the staining reaction of mucin.

3. *Bacteriological findings.*—

    (1) *Os uteri externum*   (a) *Staphylococcus aureus* (Rosenbach)

                                (b) *Staphylococcus aurantiacus* (Schröter)

                                (c) *B. coli communis*

(2) *Corpus uteri.*   Same as *os uteri externum*

(3) Right *cornu uteri,* sterile

(4) Left *cornu uteri,* sterile

(5) Right and left *tuba uterina,* sterile

(6) Left and right ovaries, sterile

4. *Diagnosis and discussion.*—

(1) Cystic uterine glands in wall of *os uteri internum*

(2) Leiomyoma in body of uterus

(3) "Ectodermoisering" of uterine epithelium (Replacement of simple columnar by stratified ectodermal, in some areas)

(4) Hydrosalpinx, both uterine tubes

(5) Sclerotic ovaries, with cystic degeneration of most medium sized and large Graafian follicles

Sterility in this case would have been absolute with only the presence of bilateral hydrosalpinx. In this, even tho clinical history is not complete, in all probability a puerperal infection followed the last parturition. This, then, may be theoretically considered as the starting point of the infection which left in its wake the irreparable pathologic changes in the uterine tubes. The cystic changes in the ovaries may or may not have significance. The leiomyoma was not sufficiently large to cause sterility had other portions of the genital tract been normal.

CASE 7

Clinical history.—Aged Holstein cow. Last parturition about September, 1918. Suffered retained placenta. Came to our attention October 19, 1920. Diagnosed chronic cervicitis with hypertrophy of external *os uteri.* Deep seated *corpus luteum* in right ovary. Cultures prepared at this time from cervix obtained from swabs showed the following flora: (a) *B. pyogenes,* (b) *B. coli,* (c) *Staphylococcus aureus,* (d) *Staphylococcus aurantiacus. Corpus luteum* removed from right ovary and cervix painted with Lugol's solution on October 30, 1920, again on November 10 and December 18, 1920. On January 10, 1921, removed a large portion of hypertrophied cervical folds, at which time also a quantity of pus was located in the uterus. The left horn was hard upon palpation. Adhesions were also noted between ovaries and uterus at this examination. Another examination on February 28, 1921, revealed a continued marked cervicitis and purulent metritis. The right ovary was the size of a lemon, and firm upon rectal palpation. The animal was pronounced incurably sterile and slaughtered March 5, 1921.

Necropsy

1. *Gross description.*—The carcass is poorly nourished. There is a large quantity of muco-purulent discharge in the vagina. The walls of the vagina are inflamed. There are two cysts in the floor of the vagina, 2 cm. in diameter. These contain a thick mucinous material. The folds of the external *os uteri* are hypertrophied. Granular, inflammatory areas, pin point in size, stud the mucous surface. The cervical canal contains much thick yellow pus. The mucosa of the body of the uterus is rather dry. The right horn of the uterus is hard and indurated and about one-third smaller than the left one. At the bifurcation of the uterus, situated above and to the right, is an adhesive mass of tissue, adherent to the serosa of the horn. At this place the wall is hard and thick. This horn contains a considerable quantity of white pus, which is creamy in consistency. The wall of the right horn is 1.5 cm. in thickness. The left uterine horn is flatulent and indurated. The wall is 1.5 cm. in thickness. It contains pus, as does the right side of the uterus. The right uterine tube is normal at the isthmus. At a distance of 2 cm. from the uterus it becomes very tortuous. It gradually enlarges until it reaches 1 cm. in diameter. It is distended with a clear serous fluid. The fimbriated end is obliterated by a mass of connective tissue. This mass is 10 cm. in width, 4 cm. in depth, and 7 cm. in length. It is covered by mesenteric fat which adheres to it and brings a loop of the small intestine in close apposition. In the center of this connective tissue mass there is considerable pus. The connective tissue first described forms the wall of the abscess. This wall is adherent to the right ovary on one side, and to the serosa of the uterus on the other side. The abscess extends into the right ovary and is responsible for its large size. The pus in the ovarian abscess is greenish, thick, and pasty, and has a nut-like odor. The left uterine tube is enlarged, and the walls are thick and hard. The right ovary is covered by dense connective tissue, being almost completely buried in the mass. It measures 7 by 3 cm. It contains an old *corpus luteum* 2 cm. in diameter. The ovary appears sclerotic. The left ovary is normal. It measures 5 by 3 by 1.5 cm. It contains a *corpus luteum* 1.5 cm. in diameter. Many small Graafian follicles are also present.

Microscopic description.—The epithelial lining of the vagina is stratified ectodermal. The outer portion shows some destruction of epithelial cells, but not pronounced. The inflammatory exudate seen grossly in the vagina is evidently drainage material from the uterus. Lying on the epithelial surface, many polymorphonuclear leukocytes are seen. The cyst described grossly is composed of a lining of simple columnar epithelium, thrown more or less into folds (Bartholin gland).

The cavity contains a faint neutral-staining, homogenous material, probably mucus. Throughout this material cholesterin clefts and fatty acid crystals are numerous. Tiny globules of neutral fat are also seen. The *cervix uteri* shows extensive superficial proliferation. This has in many instances occluded the openings of the cervical folds so that gland-like structures without outlet to the surface appear buried beneath this proliferated connective tissue. The cells of these occluded folds contain much mucus, as do also the epithelial cells of the surface mucosa. In the zone of fibrosis, many small capillaries are seen, and quite uniformly infiltrating the area are plasma cells and large mononuclear leukocytes. The body of the uterus and the cornua show marked changes in the mucosa. The lining epithelium is very irregular in its state of preservation. In one area, for a short distance, the epithelium appears as stratified ectodermal six to eight cells in thickness. It ends abruptly and is continued on each end as simple columnar epithelium. The columnar epithelium contains much mucus but the "ectodermoised" area is free of this secretion. Attached to the epithelium and infiltrating it there remain occasionally polymorphonuclear leukocytes. In some places the epithelium is necrotic. Beneath the epithelial surface the mucosa is densely infiltrated with leukocytes. Plasma cells predominate, with polymorphonuclear leukocytes and lymphocytes also numerous. They diminish in number in the deeper structures of the mucosa and young connective tissue cells become more prominent. The uterine glands are markedly atrophied. In many places the inflammatory reaction has produced proliferative changes occluding the outlet of the glands. This has resulted in dilation with retention of mucus. These have very irregular and tortuous outlines. The epithelium is low cuboidal and is not seriously damaged. Some glands show a greatly flattened epithelium surrounded by rather dense fibrillar connective tissue, and in the lumina of many, polymorphonuclear leukocytes are seen. Throughout the myometrium there are several collections of cellular infiltrations similar in character to those described for the endometrium. The mucosa near the tips of the horns is much less involved. Many normal glands still remain but superficial changes have begun which suggest the gradual transition to the chronic changes as described for the other portion of the uterus. In the left *tuba uterina* the wall is thickened, owing to the increase of connective tissue. The folds of the mucosa are greatly thickened, and many adhere to one another. In the central portion of the lumen the folds converge where they have become adherent to folds on the opposite side of the tube. Owing to this overgrowth, many folds have been brought together at their base, so that they appear as acini of glands below the connective tissue mass. All

the folds, even where adherent, are still lined by simple columnar epithelium, which contains much mucus. The connective tissue is infiltrated with lymphocytes, and in the lumina between adherent folds, polmorphonuclear leukocytes and lymphocytes are occasionally found. The right *tuba uterina* is normal at the isthmus. Above this the tube is large. The wall is much thicker and edematous. The folds of the mucosa are thickened and elongated. They converge toward the center of the lumen where they form a thick mass of edematous connective tissue, lined by simple columnar epithelium. The other folds are likewise covered by the same type of epithelium. Considerable exudate is present in the lumen of the tube and between adherent folds. This consists of inspissated serum, fibrin, and a few polymorphonuclear leukocytes and lymphocytes. The ovaries show a marked lymphocytic infiltration, which in some areas forms dense masses. The larger follicles show cystic changes, marked only by increased density of *liquor folliculi*. The smaller follicles show quite uniformly degenerative changes in the ova and the cells of the *membrana granulosa*. These changes are not marked and are difficult to interpret.

3. *Bacteriological findings.*—
   (1) The *os uteri externum*, and uterus
       (a) *B. pyogenes* (Lucet)
       (b) *Streptococcus non-hemolyticus II* (Gamma type)
       (c) *Staphylococcus aureus* (Rosenbach)
   (2) Uterine tubes. Right tubo-ovarian abscess and right ovary
       (a) *B. pyogenes*
       (b) *Streptococcus non-hemolyticus, II*
       (c) *Staphylococcus epidermidis* (Gordon)
   (3) Left ovary, sterile
4. *Diagnosis and discussion.*—
   (1) Vaginitis and cystic Bartholin glands
   (2) Chronic purulent cervicitis and metritis
   (3) Hydrosalpinx of both tubes
   (4) Right tubo-ovarian abscess
   (5) Right ovary sclerotic, cystic Graafian follicles
   (6) Left ovary shows cystic Graafian follicles

The presence again of cystic degenerative changes in the Graafian follicles is interesting. As a result of the long continued metritis, chronic changes have occurred which have left the uterus in a state of irreparable destruction with loss of breeding efficiency. The causes of sterilty are apparent.

CASE 8

Clinical history.—Holstein cow, 4 years old. Last calf born February 19, 1919, normal. Did not retain placenta. Cow has never aborted. Infectious abortion in herd five years ago. Cow has regular estrous periods. Animal was bred twelve times following birth of calf in February, 1919, and at no time did conception take place. Slaughtered as a tuberculin reactor December, 1920. No evidence of tuberculosis found at postmortem examination.

Necropsy

1. *Gross description.*—The vagina is normal except near the vulva where there is evidence of granular venereal disease. The cervical canal is open, it being possible to insert the small finger without difficulty. The uterus appears normal on its serous surface. Both uterine tubes are normal. The left ovary is normal in size. A *corpus luteum* 2 cm. in diameter is imbedded in the ovarian substance. It is hemorrhagic, many small blood vessels being present about the periphery. Two large follicles 15 mm. in diameter are present on the surface. These appear to be cystic. The right ovary is normal in size. On the upper surface there appears a cyst 1 cm. in diameter. The walls are thick. A small scar (*corpus albicans*) appears on the border of the cyst.

2. *Microscopical description.*—The vagina is normal. The cervix is normal. In the uterus the superficial glands of the mucosa are active, appearing according to Marshall's descriptions as in the period of proestrum. These glands show degeneration and desquamation of the epithelium and increased cellular and mucous exudate in their lumina. The cells of the exudate are mostly lymphocytes and large mononuclear leukocytes. Erythrocytes are not evident outside the blood vessels. The deeper glands are normal and in a state of rest. The *tubae uterinae* are normal. The ovaries appear for the most part normal, the primitive ovarian follicles are normal, as also are the larger ones that are present in the several sections taken.

3. *Bacteriological findings.*—

    (1) *Os uteri externum, corpus uteri,* and right horn

        (a) *Staphylococcus aureus* (Rosenbach)

        (b) *Staphylococcus aurantiacus* (Schröter)

        (c) *Staphylococcus candidus* (Cohn)

    (2) Left uterine horn, uterine tubes, and ovaries are sterile

4. *Diagnosis and discussion.*—In this case the only suggestions of pathological changes are obtained from study of the endometrium. The changes seen do not, however, seem commensurate with absolute

sterility. Possibly altered secretion, which can not be judged histo-logically, played an important part. Nutritional disturbances may also have been an exciting factor. Any hypothesis proposed can have no scientific support in the light of present knowledge. Cases such as these are difficult to account for. The possibility of the *corpus luteum* of the left ovary influencing conception must also be taken into account, the enucleation of which might have cleared up the condition.

CASE 9

Clinical history.—Aged Hereford cow. Several calves were born normally, after which the animal failed to conceive. Had been sterile one year when brought to our attention. Clinical examinations re-vealed nothing but cervicitis. This condition was treated regularly with Lugol's solution for two or three months. *Corpora lutea* were enucleated from time to time. Slaughtered because of sterility on December 15, 1920.

Necropsy

Gross description.—The carcass is well nourished. The external *os uteri* shows many hypertrophied folds. The cervical canal contains a thick tenacious discharge. This is transparent and glistening. In some places it is streaked with blood. In the wall of the *corpus uteri* there is a tumor 13 mm. in diameter. It is rounded and well circum-scribed. The mucosa of the uterus is normal. The walls are 8 mm. in thickness. The right uterine tube appears normal. It contains a white colored tenacious mucus. The left uterine tube is normal except at the fimbriated end, where it is adherent to the left ovary. The tube here is slightly dilated as in hydrosalpingitis. The right ovary contains many Graafian follicles. These, instead of containing a clear serous fluid, contain a mucinous one. Ovaries are normal in size. A *corpus luteum* is embedded in the ovarian substance. The *corpus luteum* is surrounded by a tough capsule, except in a small area at the surface where a small portion protrudes from the surface. The *corpus luteum* is 2 cm. in irregular diameter. In the center is a cystic cavity 4 mm. in diameter, containing a clear fluid. Over the remainder of the surface of the ovary there are many Graafian follicles. A *corpus luteum* lies on the broad ligament. It measures 1.5 cm. in diameter and is very hard in consistency. This represents a recently enucleated *corpus luteum* which is being absorbed in the peritoneal cavity.

2. *Microscopical description.*—The cervix is normal. The uterus is practically normal. A few glands of the mucosa show dilation and a flattened epithelium surrounded by rather dense circular bands of connective tissue. In others and surrounding some, lymphocytes are

seen. The glands are in a beginning state of activity. The tumor described in the wall of the *corpus uteri* is composed almost entirely of smooth muscle. It is well encapsulated. The left *tuba uterina* is normal except at the fimbriated end, where it is dilated and adherent to the ovary. The folds of the mucosa are adherent near their tips and the spaces formed between them are lined with low cuboidal epithelium. The folds are greatly stretched and thin. This gives the tube the appearance of small multiple cystic cavities. There is a precipitate in the lumina, between the folds, indicating the previous presence of a serous exudate. Only occasional collections of lymphocytes are seen in the exudate. Figure 8 illustrates this condition. The right *tuba uterina* is normal. The left ovary contains many *corpora albicantia*. The medium sized follicles are cystic, as indicated by the replacement of the normal *liquor folliculi* by a fluid precipitating much albumin and containing much material staining like mucin. Other follicles show atretic degeneration. Primitive Graafian follicles are very few in number, and the organ appears to be sclerotic. Sections obtained from the wall of the small cyst of the *corpus luteum* show it to be composed internally of a flattened layer of lutein cells, supported by a loose connective tissue framework. This is derived from ingrowths of connective tissue into the *corpus luteum* from the supporting membrane of the Graafian follicle. Beneath this the solid cords of lutein cells, with rich blood supply, are seen. The central cavity contains a small amount of debris, precipitate of the fluid it contained. Sections of the enucleated *corpus luteum,* found in the peritoneal cavity, show a uniform necrosis of all lutein cells. These appear as granular eosin-staining areas without definition. Small clear spaces left by neutral fat are abundant. The right ovary shows cystic and degenerated follicles as described for the left one. It also appears somewhat sclerotic. Some of the ovarian arterioles show hyaline degeneration of the media.

   3. *Bacteriological findings.*—

      (1) *Os uteri externum, Staphylococcus epidermidis* (Gordon)

      (2) Right *cornu uteri, Streptococcus mitis* (Alpha type)

      (3) *Corpus uteri,* left *cornu uteri,* uterine tubes, and ovaries are sterile.

   4. *Diagnosis and discussion.*—

      (1) Leiomyoma of *corpus uteri*

      (2) Hydrosalpinx of abdominal osteum of tube with adhesions to right ovary

      (3) Sclerotic changes in ovaries, and cystic degeneration of follicles

      (4) Persistent *corpus luteum* in left ovary, with central cystic degeneration.

Sterility in this case can only be accounted for histologically by the hydrosalpinx in the right *tuba uterina,* sclerotic changes in ovaries, and cystic degeneration of ovarian follicles. The persistent *corpus luteum* which formed so frequently in the left ovary was also a contributing factor. The changes seen indicate a one-time virulent infection, leaving only as a result the changes in the right *tuba uterina* and possibly the altered ovarian function. The case exemplifies further the close relationship that exists between the ovaries and sterility, involvement usually being bilateral.

CASE 10

Clinical history.—Holstein cow, about four years old. Presented at clinic for examination July 24, 1920. Past breeding unknown. The vagina was inflamed and the walls were adherent. This created a blind ending, just anterior to the urethral opening. The right ovary was found to be cystic. The cyst was approximately the size of an English walnut. This cyst was ruptured several times. The right uterine tube was enlarged, and thought to be affected with hydrosalpingitis. In the left ovary a *corpus luteum* was palpated. This was enucleated on September 1, 1920. It was impossible to dislodge it before, owing to deep embedding. Animal appeared in estrum September 3, 1920, but was not bred because of the occluded vagina. Was condemned as incurably sterile and slaughtered for food purposes December 17, 1920.

Necropsy

1. *Gross description.*—Carcass exceptionally well nourished. The vagina is closed just anterior to the urethral orifice. The stricture appears to be the result of an inflammatory reaction which brought the vaginal walls in close apposition and united them by scar tissue. The center of the stricture presents a small rounded opening which communicates with the anterior portion of the vagina. The opening is 3 mm. in diameter. Anterior to the stricture the vagina has narrowed to 1.5 cm. in width. The cervix appears normal. The vagina enlarges at the external *os uteri* so that this structure is easily accommodated. The body of the uterus is normal. The left horn of the uterus is 3 cm. in cross-diameter, at a point just anterior to the body. The right uterine horn is 5 cm. in diameter in the respective area, and continues to its extremity to be approximately twice as large as the left one. The right horn is flaccid. The uterine mucosa appears normal. The right *tuba uterina* is normal at the isthmus. It gradually enlarges until it reaches a diameter of 8 mm. at the fimbriated extremity. This enlarged area adheres to the right ovary. It contains a clear, watery, straw-colored fluid. The lumen is crossed by

strands of the mucosa which are adherent to one another, giving the lumen a multilocular appearance. The left *tuba uterina* is normal. The right ovary measures 5 cm. in length, 4 cm. in width, and 3 cm. in depth. It appears cystic. A large cyst about 2 cm. in diameter is present. It contains a clear straw-colored fluid, which coagulates upon leaving the cyst. The wall of the cyst is 4 mm. in thickness. The inner border is yellow, while the outer portion appears white. The yellow portion is 2 mm. in thickness. This represents the remains of lutein cells from a *corpus luteum* which passed through cystic degeneration instead of normal absorption. (This *corpus luteum* cyst was broken per rectum several times, and each time re-formed). The left ovary is normal in size. It contains on its surface 3 large Graafian follicles 6 mm. in diameter. There is also a *corpus albicans* on its surface measuring 2 mm. in diameter.

2. *Microscopical description.*—Over the mucosa of the vagina and adherent to it, there is considerable inflammatory exudate consisting of desquamated epithelial cells, large mononualear leukocytes, and lymphocytes and fibrin. The epithelium is intact in most places, only occasionally appearing irregularly exfoliated. Beneath the epithelium is a uniform distribution of lymphocytes and plasma cells, and occasional normal lymph follicles. The remainder of the wall appears normal. The cervix appears normal. The *corpus uteri* shows an extensive atrophy of mucous glands and a dense fibrous tissue replacement. Only occasionally are glands seen. Lymphocytes infiltrate the mucosa quite uniformly, more numerous than normal. In the cornua the epithelium is in many places necrotic and in others entirely lost. The glands of the mucosa show degeneration as evidenced by loss of epithelium, and lymphocytic infiltration into the lumina. This may correspond to proestrum as described by Marshall, but the destruction seems too extensive not to be considered pathological. The stroma of the endometrium is edematous. Glands do not appear atrophied, but simply show degenerative changes. In the lumen of the cornua there is considerable cellular debris, consisting of desquamated epithelial cells, lymphocytes, and mononuclear leukocytes. The left *tuba uterina* is normal. The right *tuba uterina* is normal at the isthmus. At the ampulla it becomes dilated and corresponds histopathologically to the descriptions previously given for hydrosalpinx. The walls are thickened to a great extent. The mucous folds do not cross the lumen, but are all flattened out and incorporated in the wall, with entire loss of epithelium. A few normal appearing folds remain. The enlarged lumen is lined by a simple flat epithelium (stretched columnar epithelium). The right ovary contains many *corpora albicantia*. Some follicles show degenerative changes. In

one the *membrana granulosa* and the *theca folliculi* have greatly atrophied, only remnants of these layers remaining. The ovum is caught in and surrounded by proliferations of connective tissue, which extend along the side formerly occupied by the *cumulus oöphorus*. In this area lymphocytes are numerous. Many follicles appear normal, while some medium sized ones appear cystic. These contain a heavy homogeneous eosin-staining precipitate, in place of the normal *liquor folliculi,* and the *membrana granulosa* is flattened out. Small primitive follicles are not numerous but appear normal. The wall of the cystic *corpus luteum* is lined by an edematous connective tissue, beneath which a thick layer of lutein cells are seen, supported by dense connective tissue. The left ovary is practically normal.

    3. *Bacteriological findings.—*

        (1) *Os uteri externum, corpus uteri,* left *cornu uteri,* uterine tubes and ovaries are sterile

        (2) Right *cornu uteri, Staphylococcus epidermidis* (Gordon)

    4. *Diagnosis and discussion.—*

        (1) Stricture of vagina resulting from vaginitis

        (2) Chronic proliferative changes in uterus with atrophy and degeneration of uterine glands

        (3) Hydrosalpinx of right *tuba uterina*

        (4) Many atretic and cystic degenerated Graafian follicles in right ovary

        (5) Cystic *corpus luteum* in right ovary

The presence of staphylococci in the right *cornu uteri* can not be regarded as responsible for the changes seen. It can best be defined as a chance invader, and not at the time of necropsy playing a pathological rôle. Sterility in this case would have been absolute with only the presence of vaginal stricture, so great were the bands of attachment. The uterine changes and hydrosalpinx are, as is the vaginal change, too, the end result of chronic infection produced most likely by streptococci or *B. pyogenes* or both. The degenerative changes described for the right ovary are interesting, but possibly not an important contribution.

CASE II

*Clinical history.—*Scrub cow, about 3½ years old. Animal was used as a control in the abortion herd at University Farm. Purchased from South St. Paul, May 20, 1918. Age at that time, 8 months. Agglutination test for infectious abortion in June, 1918, positive at 1-20, and slight at 1-50. September 1, 1918, test positive only at 1-20. Bred December 30, 1918. Pronounced pregnant February 15, 1919. Examined for pregnancy April 7, 1919. Found not pregnant. The animal was seen to have considerable blood on rear quarter two weeks previous

and was considered to have aborted. Large *corpus luteum* in right ovary was enucleated. Bred June 2, 1919. Pronounced pregnant October 23, 1919. Agglutination test for infectious abortion on November 22, 1919, was negative. A calf was born normally March 4, 1920. Agglutination test March 9, 1920, negative. Bred May 10, 1920. Pronounced pregnant August 11, 1920. Agglutination test August 13, 1920, negative. A calf was born normally February 15, 1921. Agglutination test on calf and dam was negative February 15, 1921. The calf died February 18, 1921. The cow developed a discharge from the uterus after parturition. This continued until she was slaughtered on March 4, 1921. The animal was condemned as a tuberculin reactor and as metritis had followed the last parturition, opportunity was taken for pathological and bacteriological study.

Necropsy

1. *Gross description.*—The carcass is well nourished. The mucosa of the vagina is slightly inflamed. The vagina contains a large quantity of thick, viscid, mucous discharge which is streaked with pus. The cervical canal is dilated and contains much discharge similar to that seen in the vagina. Otherwise it appears normal. The *os uteri internum* is inflamed. The body of the uterus is deeply congested. The horns of the uterus are deeply congested and each contains thick mucus, which in some places is streaked with pus. The pus is thick and yellow. The carunculae are large and prominent. The surfaces of the carunculae range from 0.5 to 2 cm. in diameter. They rise from the gland mucosae from 3 to 6 mm. The uterine tubes are normal. The ovaries are small, but appear normal.

2. *Microscopical description.*—The cervix is normal. The uterus shows considerable exudate in the lumen, lying on the epithelial surface. The exudate consists of inspissated serum, mucus, polymorphonuclear leukocytes and lymphocytes. Many desquamated epithelial cells are also present in the exudate. In the epithelium there are many polymorphonuclear leukocytes. The epithelial cells contain much mucus. The epithelium is simple columnar in type. Beneath the epithelium collections of leukocytes are numerous. These are for the most part polymorphonuclear, but lymphocytes are also numerous. The uterine glands are normal and in a state of rest. Occasional leukocytes are seen in the lumina of these glands. The blood vessels are engorged with blood. The uterine tubes are in a state of congestion. Some hemorrhage into the lumen exists. The right ovary is normal. Primitive and medium-sized follicles are numerous and appear normal in structure. In the left ovary, in the sections studied, several follicles appear in a state of atretic degeneration. Others show

a changed *liquor folliculi,* the coagulum being dense, homogeneous, and eosin-staining. Other structures of these follicles are normal. Very few normal Graafian follicles appear in the sections studied.

3. *Bacteriological findings.*—

    (1) *Uterus*   (a) *Streptococcus viridans* (Alpha type)
                (b) *Staphylococcus epidermidis* (Gordon)
                (c) *Staphylococcus aureus* (Rosenbach)
                (d) *Sarcina lutea*
                (e) *Torula rosea*
    (2) Uterine tubes, sterile
    (3) Ovaries, sterile

4. *Diagnosis and discussion.*—This can not be regarded as a case of sterility, for the animal was not sterile. It was studied in this series as an illustration of mild puerperal metritis. The left ovary shows cystic degeneration of many ovarian follicles, others being atretic. It is not known of what significance such change may be.

<center>CASE 12</center>

Clinical history.—Holstein cow, 7 years old. When 2 years old she gave birth to a normal calf. Since that time she has been sterile. Had irregular periods of estrum and when bred did not conceive. Animal was condemned because of sterility and slaughtered for food March, 1921.

<center>*Necropsy*</center>

1. *Gross description.*—The carcass is well nourished. The vagina is normal. The cervix is normal. The body of the uterus is normal. In the left horn there is a very slight amount of mucopurulent discharge. The right horn is normal. The uterine tubes are normal. The left ovary is normal. The right ovary is normal. It contains a normal *corpus luteum* measuring 2.5 cm. in width and 1.5 cm. in depth.

2. *Microscopical description.*—The cervix is normal. The uterus shows a thickened epithelium which occurs only in places, portions adjacent to the thickened areas being normal. In the thickened areas the cells are flat and stratified to 6 or 8 layers in depth. This epithelium appears as stratified ectodermal and possibly corresponds to "ectodermoisering" described by Wall. The endometrium otherwise is normal, as are also the other uterine coats. The uterine tubes are normal. The ovaries are both equally involved. They present, in several sections studied, degenerative changes of the Graafian follicles. In one section a Graafian follicle is seen with the following changes: The *liquor folliculi* is replaced by a dense coagulum taking a neutral

stain.   The epithelial cells of the *cumulus oöphorus* are mostly degenerated, a few cells of the *corona radiata,* however, still remain.   The *zona pellucida* is dark in color, and the vitellus, instead of being granular and containing vacuoles, is replaced by a dense homogeneous neutral-staining substance.   The nucleus is not present.   The cells of the *stratum granulosum* are in a state of degeneration.   Many are loosely distributed about the follicle.   Nuclei show degenerative changes, for the most part pyknosis.   Other Graafian follicles of medium size show the same dense coagulum replacing the normal light coagulum of the *liquor folliculi,* with stretching and flattening of the *stratum granulosum.*   The *theca folliculi* is greatly thickened.   Primitive ovarian follicles are numerous and appear normal.   *Corpora albicantia* are numerous.

3. *Bacteriological findings.*—

(1) Cultures from the *cervix uteri,* uterus, *cornua uteri,* uterine tubes, and ovaries remained sterile.

4. *Diagnosis and discussion.*—In this case, as in cases 8 and 9, the etiology of sterility is not clear.   The "ectodermoisering" described in the uterus does not seem a sufficient change to cause absolute sterility such as existed in this animal.   The ovarian changes, cystic degeneration, and atretic degeneration, are the only histological changes throwing any light upon the possible etiology.   But it can not definitely be agreed that this change is present in all follicles.   All organs cultured were sterile.   There may have been a mild puerperal infection following the birth of the calf, at two years of age.   Certainly at the time of necropsy, no infection existed.

CASE 13

Clinical history.—Holstein heifer, 2 years old.   Showed normal periods of estrum.   Examination early in December, 1920, to determine inability to conceive, resulted in finding an occuluded vagina and malformed uterus.   This was thought to be a case of arrested development of the genitalia.   The animal was closely bred, but not a twin. Condemned for sterility and slaughtered for food December 18, 1920.

Necropsy

1. *Gross description.*—The vagina is 5 cm. in length.   A short distance anterior to the urethral opening the walls of the vagina come together, forming an almost complete stricture.   In the center of the stricture is an opening 2 mm. in diameter.   Anterior to this, the vagina enlarges slightly.   There is no *cervix uteri.*   From the vagina proceeding anteriorly, there are two hard and fibrous tubes contained within a common capsule.   The length of these tubes, as they run parallel to one another, is 30 cm.   They separate at this point

and proceed forward at angles to one another. At a distance of 14 cm. from the dividing point, they end abruptly. The centers of these tubes have lumina 4 mm. in diameter, which near the anterior extremity dilate to 1 cm. The largest diameter of each tube is 1.5 cm. At the anterior end of each tube there is a maldeveloped uterine horn. The right horn is larger than the left, and is nearly spherical. It measures 9 cm. in length and 10 cm. in cross diameter. The walls are very thin and the horn is distended with a yellow turbid fluid. The left horn is similar in appearance to the right one. Its measurements are 9 cm. in length and 5.5 cm. in cross diameter. The uterine tubes run backward from the tip of each horn, and end in an indistinct fimbria. The right ovary is slightly larger than the left. It measures 4.5 cm. in length and 2 cm. in width. Over the surface of the organ there are many small follicles. These, instead of containing a clear, watery *liquor folliculi,* contain an opalescent semi-solid fluid, probably an expression of small Graafian follicle cysts. The left ovary is also cystic and contains a *corpus luteum* 3 cm. in depth and 2 cm. in width.

2. *Microscopical description.*—Sections through the remains of the Müllerian tubes show a lining of low cuboidal epithelium, in most places simple, in some areas stratified. Beneath the epithelial surface the connective tissue is dense and consists for the most part of collagenous fibrils. A few large simple tubular glands are occasionally seen. The inner surface of the tubes is thrown into low, rounded folds. Smooth muscle is distributed throughout the connective tissue and is more abundant in the deeper structures. In the partially developed uterus the mucosa is lined throughout with a thick stratified ectodermal epithelium. Beneath this is a thick coat of connective tissue distributed evenly along the mucosa. This tissue is exceedingly edematous. The uterine glands lie beneath this coat of connective tissue. They are surrounded by dense connective tissue bands and the epithelium is low columnar. Some contain much mucus. The surface of the mucosa is thrown up into small irregular folds. Differentiation into gland mucosa and carunculae does not appear. The muscular coat is thin. The entire thickness of the mucosa does not exceed the ordinary development of the endometrium of a normal uterus. The uterine tubes appear normal in structure. In the ovaries medium sized Graafian follicles are exceedingly numerous. These show quite uniformly a *theca folliculi* of increased thickness, a quite normal appearing *stratum granulosum,* and a thick homogenous, neutral-staining coagulum of the *liquor folliculi.* In the several sections studied, no ova are present. Small primitive follicles are few in number.

3. *Bacteriological findings.—*

(1) Cultures prepared from the right *cornu uteri,* left *cornu uteri,* and ovaries, sterile

4. *Diagnosis and discussion.*—A case of absolute sterility from arrested development of the genitalia. Multiple cystic degeneration of the follicles, as described here, is frequently seen in the ovaries of young girls. These correspond histologically to the cystic changes described for ovaries in other cases herein reported.

CASE 14

Clinical history.—Holstein heifer, 2 years old. Showed normal periods of estrum. Examination early in December, 1920, in order to determine inability to conceive, resulted in finding an occluded vagina and rudimentary uterus. This was thought to be a case of arrested development of the genitalia. The animal was closely bred, but not a twin. Condemned for sterility and slaughtered for food, December 18, 1920.

Necropsy

1. *Gross description.*—The vagina is 7 cm. in length, the anterior extremity being completely closed. There is no *cervix uteri.* The vagina communicates anteriorly with two tubes, as in case 13. The tubes are contained within a common tough and fibrous sheath. The tubes themselves are very fibrous. The lumen is collapsed, and almost adherent from side to side. It does not communicate with the cavity of the uterus or vagina. The tubes continue forward as those described in case 13, each one ending at a partially developed uterine horn. The right uterine horn is 8 cm. in length and 4 cm. in cross diameter. The walls are very thin. The horn is distended to about half its capacity with a turbid, yellow, watery fluid. The left horn is extremely rudimentary. It measures 2.5 cm. in length and 1.5 cm. in cross diameter. The walls are thick and a yellow fluid is contained in the lumen. The right uterine tube is normal. The left uterine tube is short but appears normal. The right ovary is 5 cm. in length and 3 cm. in width. It contains a *corpus luteum* 24 mm. in width and 19 mm. in depth. Over the surface there are many small cystic follicles. The left ovary is 3 cm. in length and 2 em. in width. It contains many small cystic follicles.

2. *Microscopical description.*—The persistent Müllerian tubes show a small lumen lined with stratified ectodermal epithelium supported by a dense connective tissue of collagenous type. Occasional glands are present in this area. Smooth muscle is distributed through the lower portion, but is not great in amount. The serosa is composed of a thick layer of areolar tissue. The partially developed *cornua uteri*

are similar in structure to those described for case 13. The uterine tubes are normal. The ovaries show many *corpora albicantia* distributed throughout the cortex. Primitive follicles are normal. Nearly all medium sized and large Graafian follicles show cystic degeneration, marked by a dense coagulum replacing the granular coagulum of the *liquor folliculi*. Ova are not seen in any of these follicles. The cells of the *stratum granulosum* do not appear to be damaged.

3. *Bacteriological findings.*—

    (1) Cultures of the *cornua uteri*, uterine tubes, and ovaries remained sterile.

4. *Diagnosis and discussion.*—Partial arrested development of genital organs and cystic degenerative changes in Graafian follicles.

CASE 15

1. *Clinical history.*—Aged Holstein cow. A normal calf was delivered on November 20, 1920. The parturition was difficult owing to a breech presentation. Purulent metritis and cervicitis developed following parturition. On December 6, 1920, swabs were taken from the uterus and cultures prepared. From this material the following organisms were isolated: 1. *Bacillus pyogenes* (Lucet), *Staphylococcus aureus* (Rosenbach), and *Streptococcus pyogenes* (Beta type). On the same date a retained *corpus luteum* was palpated in the right ovary and enucleated. The right uterine horn was elongated and much enlarged, and a considerable quantity of thick yellow pus could be massaged from it. The cervix was also much inflamed. The uterus was flushed with a mild antiseptic and the cervix painted with pure Lugol's solution at ten-day intervals. Improvement was continuous and the animal was pronounced ready to breed on March 31, 1921. The periods of estrum were at this time regular. Animal apparently normal but not pregnant June 14, 1921.

2. *Diagnosis and discussion.*—(1) Purulent cervicitis and metritis, acute in type, and caused by *B. pyogenes,* and *Streptococcus pyogenes.* These organisms were found on three examinations. It will be interesting to note whether changes have been produced that will render the animal permanently incapable of reproduction. It is too early at this time to make a definite prognosis, except that clinically everything seems normal.

NOTE.—This animal is now pregnant from December 24, 1921, service.

CASE 16

Clinical history.—Aged Guernsey cow. Delivered a normal calf in June, 1920. The placenta was retained, following which she developed a severe purulent metritis. It received little attention until January 13, 1921, when examination revealed a deeply seated *corpus luteum* in the right ovary. The *cervix uteri* was inflamed and the

cervical canal partly dilated. The uterus was enlarged, flaccid, and abdominal in position. The persistent *corpus luteum* was enucleated on January 17, 1921. Following this operation the uterus began to contract, and within 24 hours 4 to 5 liters of thick, creamy pus was evacuated. The pus was very malodorous. Cultures were prepared from this discharging material. From this exudate the following organisms were isolated: (1) *B. pyogenes* (Lucet) and (2) *Streptococcus viridans* (Alpha type). Following the operation upon the *corpus luteum* the animal was very uneasy and failed to eat her evening meal. The discharging pus continued for 3 or 4 days. Examination on January 24 showed the uterus to be pelvic in location, almost normal excepting for a slightly enlarged right horn. The cervix was inflamed and was painted with Lugol's solution. The uterus was massaged. The animal was allowed to rest one month. On February 28 an examination showed the right horn of the uterus still slightly enlarged. The uterus was irrigated with a 2 per cent solution of therapogen. Examination on March 7 found all organs normal and cow showing symptoms of estrum. Discharged from the clinic March 9, 1921, apparently recovered. Examination in May revealed the development of a slight tubo-ovarian abscess. The animal was not pregnant.

2. *Diagnosis and discussion.*—Pyometra, cervicitis, and tubo-ovarian abscess, the etiology of which is (1) *B. pyogenes* (Lucet) and (2) *Streptococcus viridans* (Alpha type).

Note: This cow now (March 13, 1922) comes in heat regularly, discharge has ceased, and she is thought to be with calf.

CASE 17

1. *Clinical history.*—Holstein cow, about 5 years old. Normal calf was born November 15, 1920. Following parturition the placenta was retained. Purulent metritis developed but received no special attention until March 28, 1921. Examination revealed a much enlarged uterus (pyometra), cervicitis, cystic left ovary, and *corpus luteum* in right ovary. The cyst was ruptured and the *corpus luteum* enucleated on this date. Pus began to flow freely from the vagina within 24 hours after enucleating the persistent *corpus luteum*. The removal of the *corpus luteum* allowed the uterus to undergo normal involution. The pus which came from the uterus was yellow in color and streaked with blood and was very malodorous. Swabs were taken from the uterus and cultures prepared. The following organisms were isolated: (1) *B. pyogenes* (Lucet), and (2) *Staphylococcus epidermidis* (Gordon). The uterus was washed with a 2 per cent solution of therapogen on this date, and after being emptied, the entire organ could be placed beneath the hand, by rectal palpation. Examination on April 1, 1921, showed the uterus to have better muscular tone. The cervix was still

slightly inflamed. The cervix was treated with Lugol's solution. Examination on April 2 showed the animal to be in estrum. The left uterine horn was normal, the right uterine horn was still slightly inflamed. Examination on April 4 showed the left uterine horn to be practically normal, and the right horn still enlarged and flaccid. On this date the uterus was massaged and the cervix was treated with Lugol's solution. Examination on April 7 showed the right uterine horn to be smaller and with better muscular tone. The cervix was treated with Lugol's solution and the uterus washed with 2 per cent solution of therapogen. Following this it was massaged. On April 9, examination revealed a normal uterus, a *corpus luteum* in the left ovary, a contracted cervix, and a small quantity of pus in the vagina. The *corpus luteum* was enucleated. The animal appeared in estrum following this and was discharged from the clinic soon after.

2. *Diagnosis and discussion.*—Pyometra and cervicitis following parturition, and caused by *B. pyogenes* and *Staphylococcus epidermidis*. The animal has apparently recovered.

NOTE.—Later she was sold at public sale as a healthy individual.

CASE 18

1. *Clinical history.*—Holstein cow, 6 years old. Delivered a normal calf November 28, 1920. Following parturition the animal retained the placenta, but it was promptly removed. Following this the animal did not appear in estrum. While decumbent, a thick creamy discharge could be seen coming from the vagina. The animal was presented in the University clinic for treatment on March 28, 1921. Examination on March 28 revealed a large, elongated uterus, hanging down over the brim of the pelvis. In the right ovary was a large persistent *corpus luteum*. This was enucleated. On the following day the animal began to discharge large quantities of pus from the uterus. It was thick and creamy in consistency and light yellow in color. Swabs were taken from the uterus at this time and cultures prepared. The following organisms were isolated: (1) *B. pyogenes* (Lucet), (2) *Streptococcus viridans* (Alpha type), (3) Streptococcus (Gamma type), (4) *Staphylococcus aureus* (Rosenbach), and (5) *Staphylococcus epidermidis* (Gordon). The uterus gradually returned to normal. On April 22 a clinical examination of the genitalia was made. The right horn of the uterus was slightly enlarged and upon massage a small quantity of pus could be expressed. The uterus was washed with a 2 per cent solution of therapogen. On April 25 the uterus was found practically normal. The horns were of equal size. The organ was massaged per rectum until a clear mucus was discharged from the vagina. The cervix was still slightly inflamed and the cervical canal was partially open. The animal was pronounced

practically normal and discharged from the clinic on the following day. The animal has been bred and is now pregnant.

2. *Diagnosis and discussion.*—Pyometra and cervicitis caused by *B. pyogenes, Streptococcus viridans,* and staphylococci. Recovery has apparently been complete, but definite knowledge of this can not be had till later, when it is definitely known that a fetus has been carried through the normal period of gestation.

CASE 19

Clinical history.—Cow without clinical history, obtained from the abattoir at South St. Paul.

Necropsy

1. *Gross description.*—The vagina is normal. The cervix is normal. The right horn of the uterus is approximately 8 cm. in diameter, at a point just anterior to the *corpus uteri.* It is hard, upon palpation. It gradually tapers toward the tip of the horn. The lumen of the horn contains about 100 cc. of a yellowish, granular exudate. The mucosa (endometrium) and myometrium are extensively invaded with small yellow tubercles. Many are caseous and others calcified. On the mucous membrane these form small yellow, hard, rounded prominences. The left uterine horn is normal in size except near the tip, where there is a hard mass 4 cm. in diameter, and 2 cm. in length. This contains many small calcified tubercles. There is no exudate in the lumen of this horn. The right uterine tube is normal in appearance at the isthmus. Toward the ampulla it is dilated to 4 mm. and is very hard, upon palpation. It is yellow in color. The left uterine tube presents a similar involvement. The right ovary contains a cyst 17 mm. in diameter, and at the opposite end of the ovary, a large *corpus luteum.* The *corpus luteum* is 2 cm. in diameter. The center presents a cystic cavity 4 mm. in diameter. The left ovary is normal. There are many soft tubercles, gray in color, upon the broad ligament and surrounding the uterine tubes and ovaries. The mass is so dense that dissection of these organs from it is very difficult.

2. *Microscopical description.*—The uterus shows many tubercles throughout the wall, especially in the endometrium. The smaller ones have no central necrosis. These are composed of endothelioid cells and many giant cells are also seen. A zone of lymphocytes surrounds the tubercle. Larger ones are similar, with central necrosis. The stroma of the endometrium is infiltrated densely with lymphocytes. The glands are for the most part normal. A few are dilated, showing a thinned epithelium and fibrous thickening of the *membrana propria.* In the muscularis several large necrotic tuberculous masses are seen. The central portion shows extensive calcification, surrounding which

is a wide area of necrosis. Around the necrotic area are massed large numbers of endothelioid cells and many giant cells. Intermixed with and especially massed at the outer periphery there are numerous lymphocytes. The larger tubercles are well encapsulated with connective tissue. The larger tubercles of the muscularis extend also into the endometrium almost to the uterine epithelium.

Areas of the uterus where no tubercles appeared to be present grossly, are also normal microscopically.

The uterine tubes are practically destroyed by the tuberculous process. The tubes are slightly larger than normal. The mucosa is entirely destroyed. No normal structures remain. There is necrosis of all layers of the muscular coat. Around the necrotic material a thick layer of endothelioid cells is prominent, throughout which a few lymphocytes and fibroblasts are seen. A few giant cells are also present. The outer circular muscular fibers are still intact. Some sections show portions of tubal epithelium in a fairly good state of preservation, and others with necrotic remnants still present. In these areas there is extensive lymphocytic infiltration of the mucosa, with exudate consisting of coagulated serum and lymphocytes in the lumen. The serosa shows numerous tuberculous adhesions about it.

3. *Diagnosis.*—Advanced miliary tuberculosis of the uterine tubes, uterus, and parauterine tissues.

EXPERIMENTAL INOCULATIONS WITH *BACILLUS PYOGENES*

Two heifers were secured for experimental work with *B. pyogenes*. An attempt was made to infect these animals with recently isolated strains of the organism. Heifer No. 1 was in the eighth month of pregnancy, when 5 cc. of a serum bouillon culture of *B. pyogenes* from case 17 was introduced into the jugular vein (3 weeks before parturition). No observable symptoms of disease resulted. The animal carried the calf to maturity and two weeks after parturition the necropsy revealed a normal genital tract, free of bacteria. No other pathologic lesions were found. Heifer No. 2 was non-pregnant and 15 cc. of a bouillon culture of *B. pyogenes* from case 18 was introduced into the uterus. The animal developed no observable symptoms of disease and necropsy revealed a normal genital tract, practically free of bacteria. These cases illustrate the resistance of the normal body to infection, and the necessity of a predisposing cause. The prevalence of *B. pyogenes* in nature is not known. It must inhabit the animal's body and develop pathogenic characters when resistance for some reason is reduced. The inability to interfere with pregnancy is also noteworthy.

Laboratory animals were not inoculated with *B. pyogenes*. Time did not permit pathogenicity studies on small animals. The pathogenicity of *B. pyogenes* for laboratory animals has been thoroly demonstrated. According to Berger (61) and Holth (62), rabbits are the most susceptible of the small laboratory animals to experimental infection with *B. pyogenes*. Guinea pigs are less susceptible, and mice least so. Brown and Orcutt (48) were able to infect rabbits quite readily, the characteristic lesions produced being abscesses in various parts of the body.

SUMMARY AND CONCLUSIONS

I. BACTERIOLOGICAL

In the course of the bacteriologic investigations, standard works have been consulted for classification. Each organism was isolated in pure culture and then subjected to systematic study for identification. In the study of staphylococci the work of C. E. A. Winslow (54) et al, on "Notes on the Classification of the White and Orange Staphylococci," has been the basis of identification. Streptococci were at first identified according to Hollman's (55) classification and in the later work the identification was based solely on the reaction to blood agar. For the latter the monograph of James Howard Brown (56) has been followed carefully. In the studies on *B. pyogenes* the works of Lucet (46), Künnemann (47), Grips (52), Glage (53), and Ward (64) were consulted. For identification of *B. pyogenes* the work of Brown and Orcutt, "A Study of Bacillus pyogenes," has been the basis of classification (48). In addition to this, two rabbits were immunized with separate strains of *B. pyogenes*. Serum from these rabbits agglutinated all strains of the organism to an equal degree. The tables on pages 84 and 86 show the prevalence of organisms as they appear in the nineteen cases studied.

It is confusing in interpreting results in Table I to have such a large group of streptococci. All strains, excepting *Streptococcus pyogenes* and *Streptococcus anginosus* are of the non-hemolytic types (Alpha and Gamma). These two, however, fall into the group of hemolytic streptococci (Beta type).

It will be seen in careful study of the material presented that the organisms most important in infections of the genital tract of the cow are streptococci and *B. pyogenes*. These types are responsible for the greater number of infections. In all cases of severe non-specific metritis and other suppurative processes about the genitalia, *B. pyogenes* combined with streptococci, or the latter alone, have been isolated.

Other organisms are not regarded as playing a primary rôle. Unless the bacteriologic study is made during the progress of active infection, these types as well as others will most often not be found. In such cases one views only the results of infection, the active process having subsided. It is for this reason that in nearly all cases when no gross evidence of active inflammation exists, the genital tract is sterile. The vagina, *cervix uteri,* and *corpus uteri* must be excepted.

Organisms are not normally harbored as commensals in the internal genitalia of the cow, with exceptions as already made. Case 6 is an unparalleled example of this. Hydrosalpinx, the end result of active inflammation, existed, cultures from which were sterile. Case 10 also illustrates the point. Many other examples of a bacteria-free genital tract may be found in the case reports, and as compiled in Table I. The absence of *B. abortus* (Bang) supports the previous view, that it is not found in puerperal infections that persist for any length of time, and that it does not persist, so far as is known, in the genitalia of the cow. *B. abortus* was not isolated from any of the cases studied.

TABLE I
COMPILATION OF BACTERIOLOGIC RESULTS

GENITAL ORGAN	CASE NUMBER																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Vagina	1 5 14	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q
Os uteri externum	1 5 14	q	q	q	q	1 2 5	1 10 13	1 2 4	3	o	q	q	y	y	11 13	13 15	13 15	1 3 13 15 19	q
Corpus uteri	o	3 5 12 13	o	o	o	1 2 5	q	1 2 4	o	o	1 3 15 17 19	o	y	y	11 13	13 15	13 15	1 3 13 15 19	20*
Right cornu uteri	o	3 5 12 13	13	o	13	o	3 10 13	1 2 4	12	3	1 3 15 17 19	o	o	c	q	q	q	q	20*
Left cornu uteri	o	3 5 12 13	o	o	o	o	3 10 13	1 10	o	-o	1 3 15 17 19	o	o	o	q	q	q	q	20*
Right uterine tube	o	3 5 12 13	o	o	4 9 13	o	3 10 13	o	o	o	o	o	q	o	q	q	q	q	20*
Left uterine tube	o	3 5 12 13	q	q	o	o	3 10 13	o	o	o	o	o	q	o	q	q	q	q	20*
Right ovary	o	2 12	o	o	o	o	3 10 13	o	o	o	o	o	o	o	q	q	q	q	q
Left ovary	q	o	q	q	o	o	o	o	o	o	o	o	o	o	q	q	q	q	q
Ovarian cysts	o	o	o	o	13	o	o	4	o	o	o	o	o	o	q	q	q	q	q
Ovarian abscess	y	2 12	y	y	13 9	y	3 10 13	y	y	y	y	y	y	y	q	q	q	q	q
Periuterine abscess	y	y	7 13	4 8 13 16	y	y	y	y	y	y	y	y	y	y	q	q	q	q	q

Explanation of Symbols in Table I

o—sterile
q—not cultured
y—structure not present
1—*Staphylococcus aureus*
2—*Staphylococcus aurantiacus*
3—*Staphylococcus epidermidis*
4—*Staphylococcus candidus*
5—*B. coli communis*
6—*B. coli communior*
7—*Streptococcus anginosus*
8—*Streptococcus fecalis*
9—*Streptococcus ignavus*
10—*Streptococcus non-hemolyticus* ii

11—*Streptococcus pyogenes*
12—*Streptococcus mitis*
13—*B. pyogenes*
14—*B. subtilis*
15—*Streptococcus viridans*
16—*B. proteus*
17—*Sarcina lutea*
18—*Torula rosea*
19—*Streptococcus* (Gamma type)
20—*B. tuberculosis**

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*—stain only

CASE II
SUMMARY OF BACTERIOLOGIC RESULTS INCLUDING ALL CASES

ORGANISM	TIMES FOUND	CASE NUMBER																		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Streptococcus Alpha type	8	—	+	—	+	+	—	—	−	+	—	+	—	—	—	—	+	+	+	—
Streptococcus Beta type	2	—	—	+	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—
Streptococcus Gamma type	4	—	—	—	—	—	—	+	+	—	—	+	—	—	—	—	—	—	+	—
B. *pyogenes*	9	—	+	+	+	+	—	+	—	—	—	—	—	—	—	+	+	+	+	—
Staphylococcus aureus	6	+	—	—	—	—	+	+	+	—	—	+	—	—	—	—	—	—	+	—
Staphylococcus all other types	10	—	+	—	+	+	+	+	+	+	+	+	—	—	—	—	—	—	+	—
B. *coli*	3	+	+	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—
B. *tuberculosis*	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+*
B. *proteus*	1	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sarcina lutea	1	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—
Torula rosea	1	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—

* B. *tuberculosis,* by stain; organs not cultured.

TABLE III
SUMMARY OF BACTERIOLOGIC RESULTS IN CASES OF SUPPURATION

ORGANISM	TIMES FOUND	CASE NUMBER											PER CENT PRESENT
		2	3	4	5	7	11*	15	16	17	18	19†	
B. *pyogenes*..................	9	+	+	+	+	+	—	+	+	+	+	—	81.8
Streptococcus Alpha type.....	7	+	—	+	+	—	+	—	+	+	+	—	63.6
Streptococcus Beta type......	2	—	+	—	—	—	—	+	—	—	—	—	18.1
Streptococcus Gamma type....	3	—	—	—	—	+	+	—	—	—	+	—	27.2
Staphylococcus aureus........	3	—	—	—	—	+	+	—	—	—	+	—	27.2
Staphylococcus other types....	6	+	—	+	+	+	+	—	—	—	+	—	54.5
B. *coli*......................	2	+	—	—	—	+	—	—	—	—	—	—	18.1
B. *tuberculosis*‡.............	1	—	—	—	—	—	—	—	—	—	—	+	9.0
B. *proteus*..................	1	—	—	+	—	—	—	—	—	—	—	—	9.0

* Case 11, mild puerperal metritis of short duration; healing would probably soon have occurred.

† Case 18, tuberculous metritis and salpingitis.

‡ By stain only; cultures not made.

2. PATHOLOGICAL

The frequency with which one views degenerative changes in the ovaries of sterile cows can not be disregarded. It seems that in all cases of infection about the genital tract, multiple cystic degeneration of medium sized Graafian follicles is an almost constant finding. Until more study is made, especially on normal animals as controls, no definite statement can be made. The uterine tubes, because of their many folds and crypts and their delicate structure, offer the most favorable site for persistence of infection. Chronic changes in the genital tract are most frequent in this location and are usually seen in the form of hydrosalpinx. In the uterus chronic changes do not readily occur. Only after severe infection over a long period of time are sufficient changes produced to render the organ incapable of serving its natural use. It does not seem as readily susceptible to persistence of infection as do the uterine tubes. The changes noted in the uterus are fibrosis, cystic dilation of glands, atrophy of glandular epithelium, thickening of uterine epithelium, and various others. The *cervix uteri*, like the uterine tubes, offers a favorable site for bacterial reproduction. The folds of the mucosa are deep and in the crypts bacteria may gain entrance and multiply. Altho accessible to treatment, the deep crypts allow infection to persist, and often extend to other portions of the genital tract. Hypertrophy of cervical folds is the most constant chronic change. The vagina, because of its smooth stratified epithelial surface, is not readily infected. It may harbor pathogenic types of bacteria, as commensals, on its surface, in its accessory glands, in the subepithelial lymph follicles, or in the urethral orifice. It is suggested that the vagina and accessory structures may be the reservoir for organisms which infect the genital tract of the cow, including *B. abortus*, and other types which cause congenital (prenatal) infections. The route of infection may be through the lymphatic system, which is most highly developed about the female genital tract. The occurrence of parauterine and periuterine infections seems to support this view.

Nineteen cases have been studied and presented. The theory of infection does not explain all cases of sterility. Where no evidence of infection, past or present, exists, and the animal is sterile, the ovaries must be looked to as the cause of the condition, except of course, where malformation of the genitalia exists.

ACKNOWLEDGMENTS

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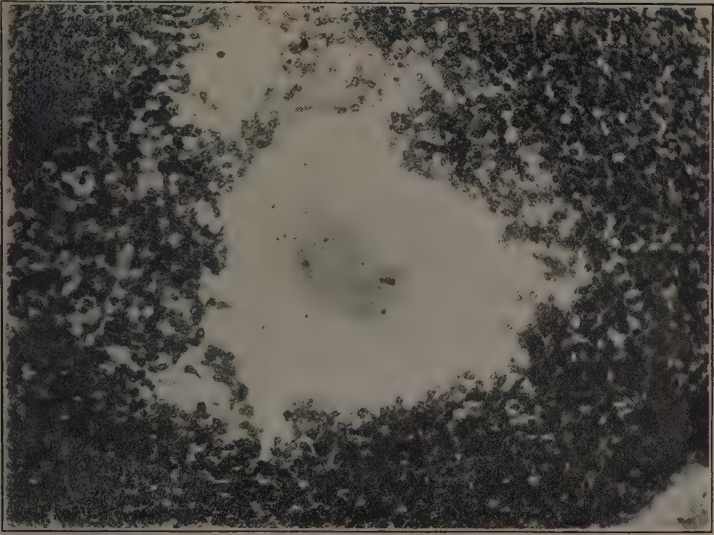
Fig. 1. Degenerative Change in Graafian Follicle, Case 5
Note proliferation of cells of *stratum granulosum*.
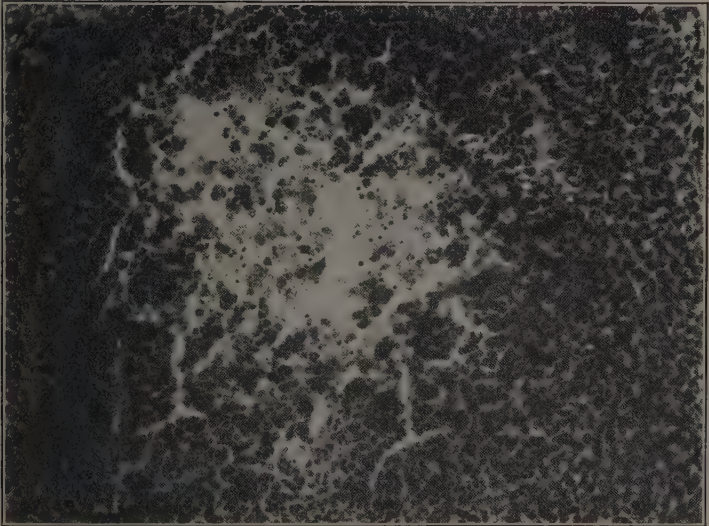
Fig. 2. Graafian Follicle Showing Degenerative Change, Case 1
Note thickening of *stratum granulosum* and *theca folliculi*.
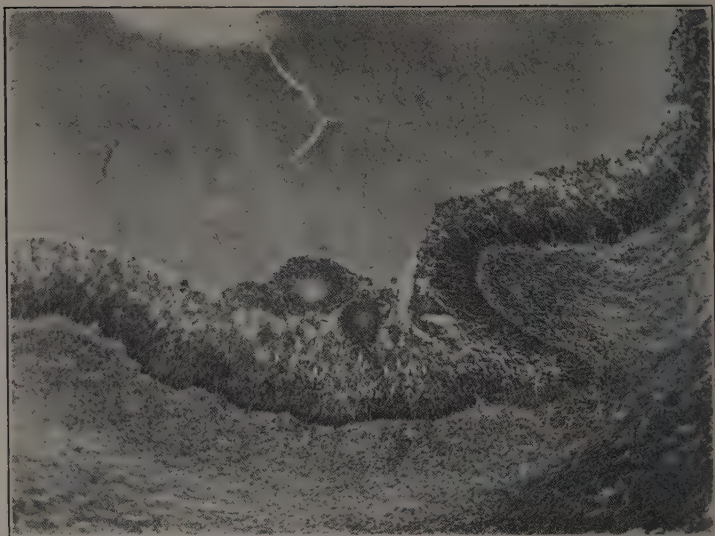
Fig. 3. Cystic Degeneration of Graafian Follicle, Case 5

Note dense coagulum replacing normal *liquor folliculi* and degenerative changes in cells of *stratum granulosum* (not marked in this case).
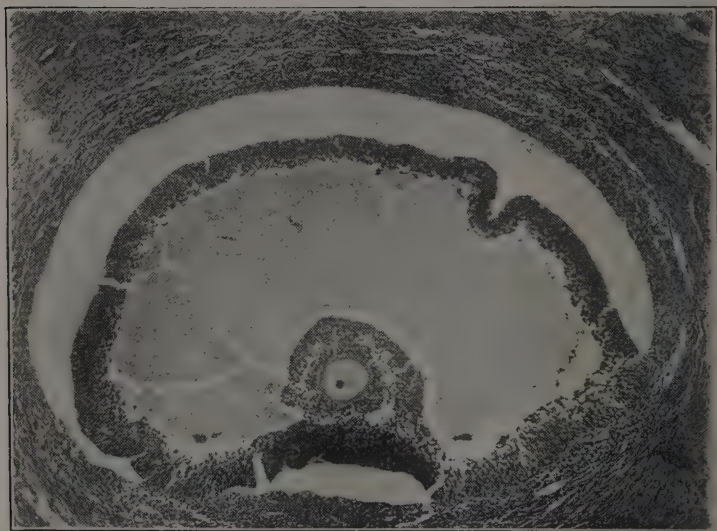
Fig. 4. Normal Graafian Follicle, Case 3

Note the granular character of the coagulated *liquor folliculi*. The pulling of the *stratum granulosum* from the *theca folliculi* is an artefact.
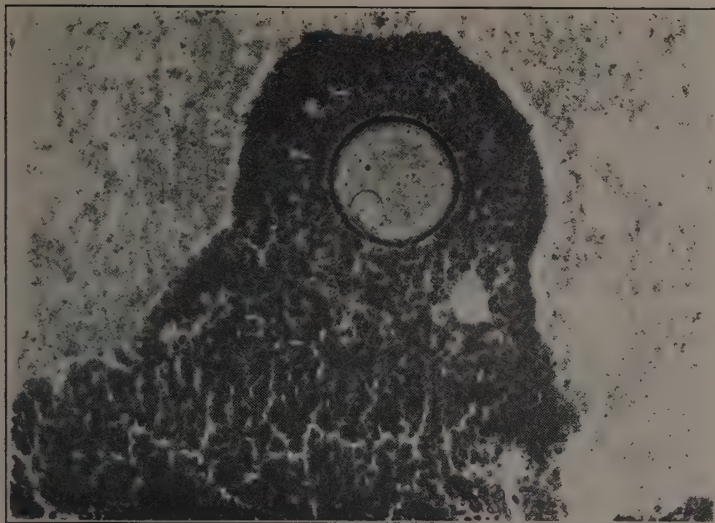
Fig. 5.   Normal Follicle, Case 2

Showing ovum surrounded by the cells of the *cumulus oöphorus*.   Note the granular character of the *liquor folliculi* coagulum.
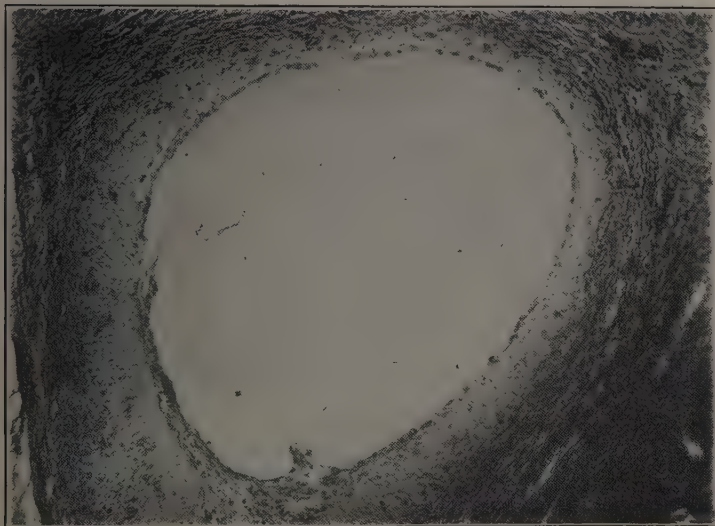
Fig. 6.   Small Cystic *Corpus Luteum,* Case 5

Lutein cells have undergone hyaline change.   Cyst surrounded by *corpus albicans*.   Fluid contains neutral fat.
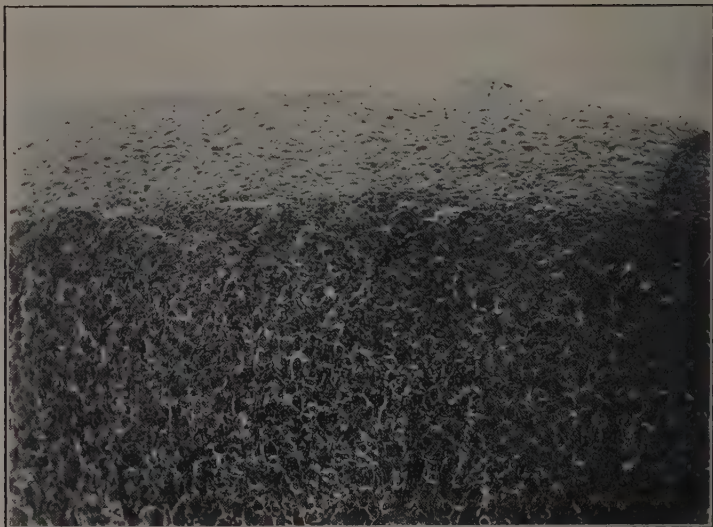
Fig. 7. Section Through Wall of Old *Corpus Luteum* Cyst, Case 10
Note connective tissue and lutein cells.
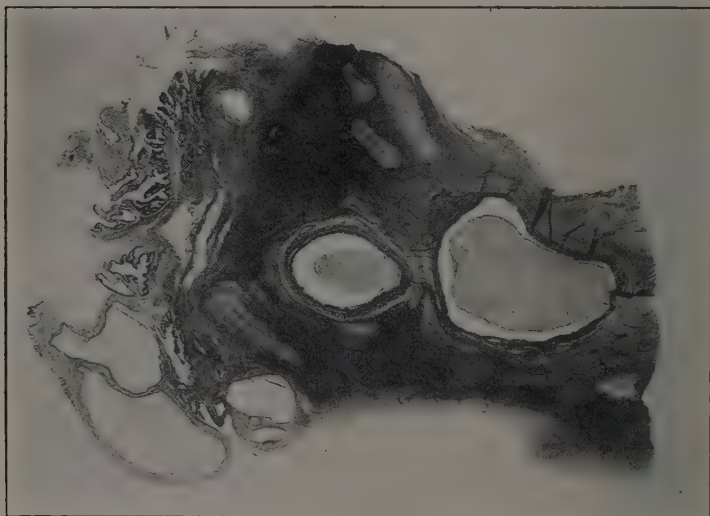
Fig. 8. Section Through Ovary, Case 9
Note uterine tube adherent to ovary, the multilocular cavities characterizing hydrosalpinx. Two Graafian follicles showing cystic degeneration are seen in the ovary.
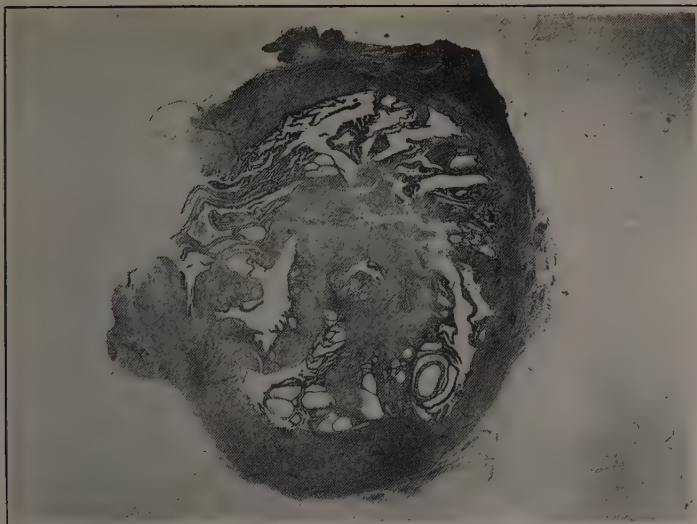
Fig. 9.   Low Power of Uterine Tube, Case 5
Hydrosalpinx, early stage.

Fig. 10.   Hydrosalpinx, Case 5
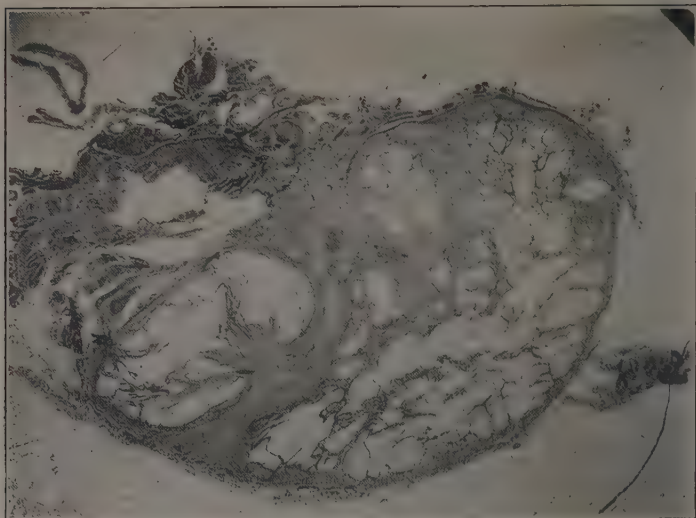
Fig. 11. Section Through Uterine Tube, Case 6
Hydrosalpinx, later stage. Note atrophy of many interlocking folds.
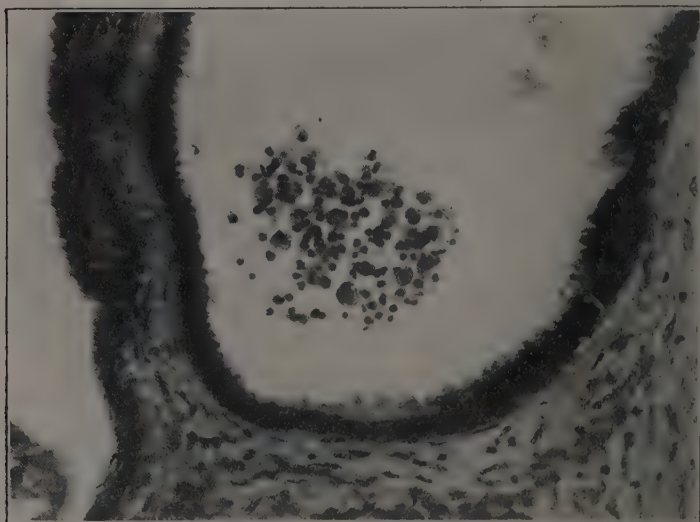
Fig. 12. Section Through One of the Cystic Pockets. Hydrosalpinx, Case 5
Note proliferation of connective tissue and epithelium. Exudate in lumen is composed of polymorphonuclears, lymphocytes and desquamated epithelium.
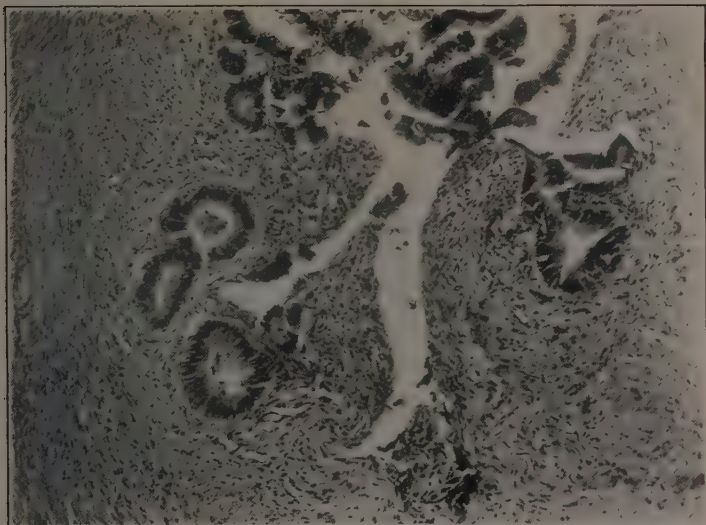
Fig. 13. Very Mild Salpingitis, Case 4

Epithelium is abnormally desquamated and in the wall many lymphocytes are seen.
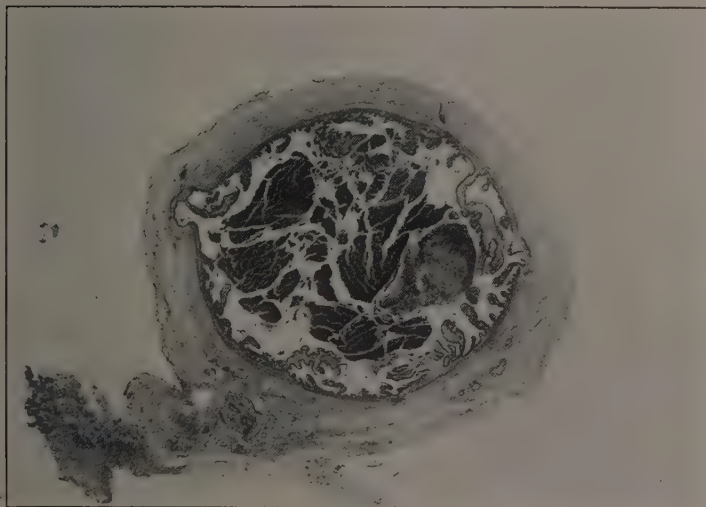
Fig. 14. Purulent Salpingitis, Case 2

Low-power section of uterine tube. Note the purulent exudate in the lumen.

Fig. 15. Section Through Caruncula, Case 7

Note great thickening of uterine epithelium, stratified over caruncula and simple columnar at the border. "Ectodermoisering."
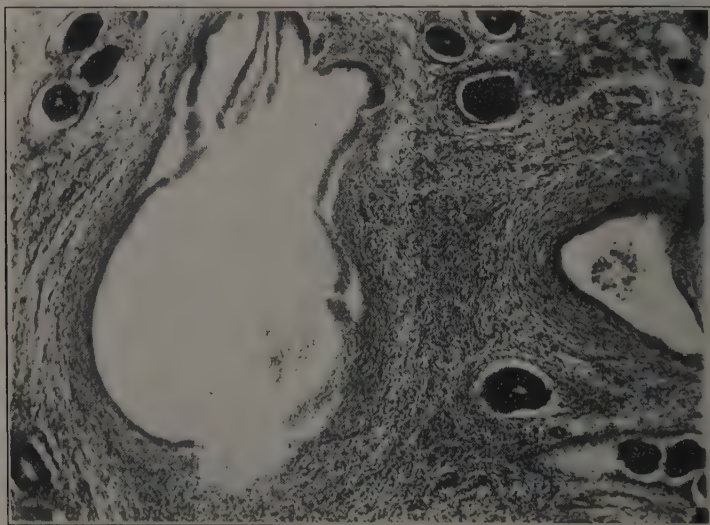
Fig. 16. Dilated Uterine Glands, Case 2

There is considerable destruction of the glandular epithelium. Other deeply stained glands in same section remain normal.
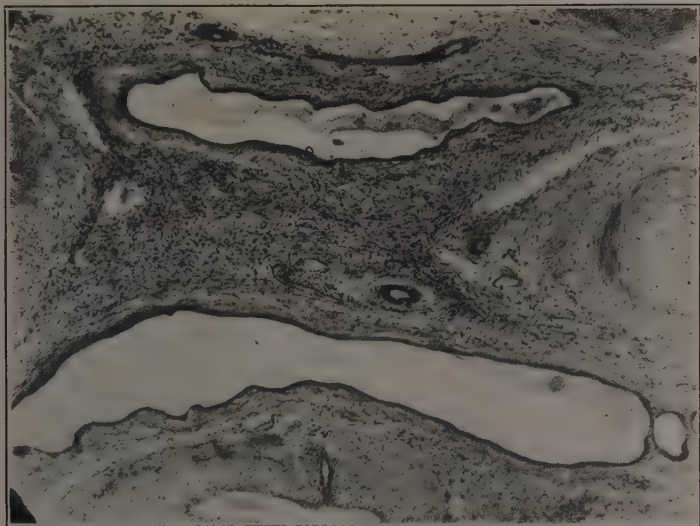
Fig. 17. Section Through Wall of Uterus, Case 7

Note fibrosis of uterine stroma, dilation of uterine glands and atrophy of glandular epithelium.
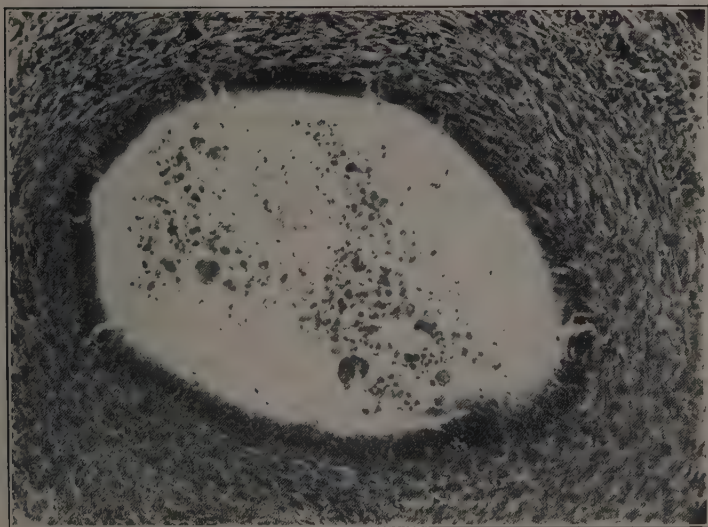
Fig. 18. Section Through Dilated Uterine Gland, Case 2

Note connective tissue proliferation surrounding gland and exudate in its lumen, mostly polymorphonuclears.
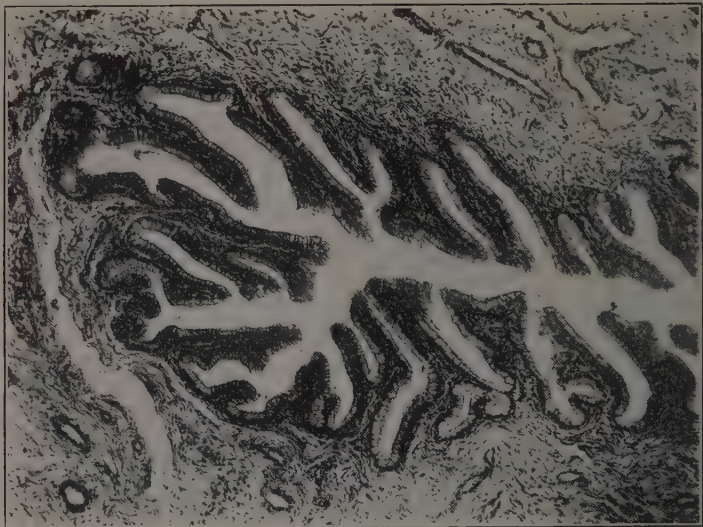
Fig. 19. Normal Fold in *Cervix Uteri*, Case 5

These folds may harbor pathogenic bacteria. In them infection is persistent when once started.
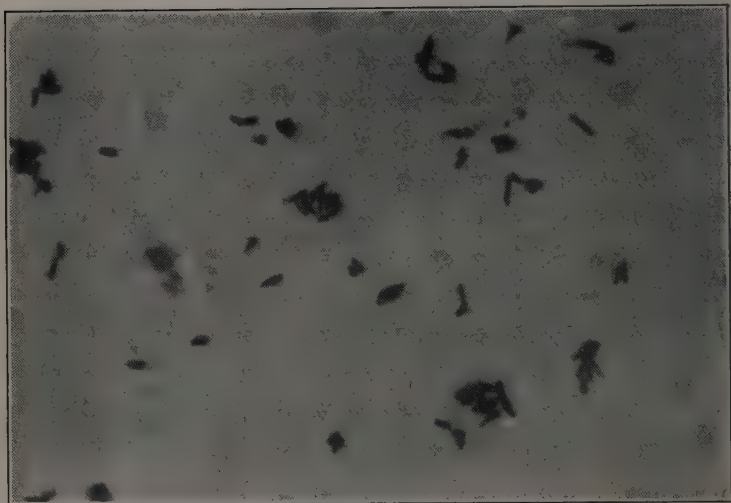
Fig. 20. *B. pyogenes*, Case 18

Note the characteristic clusters, parallel grouping and diphtheroid types.
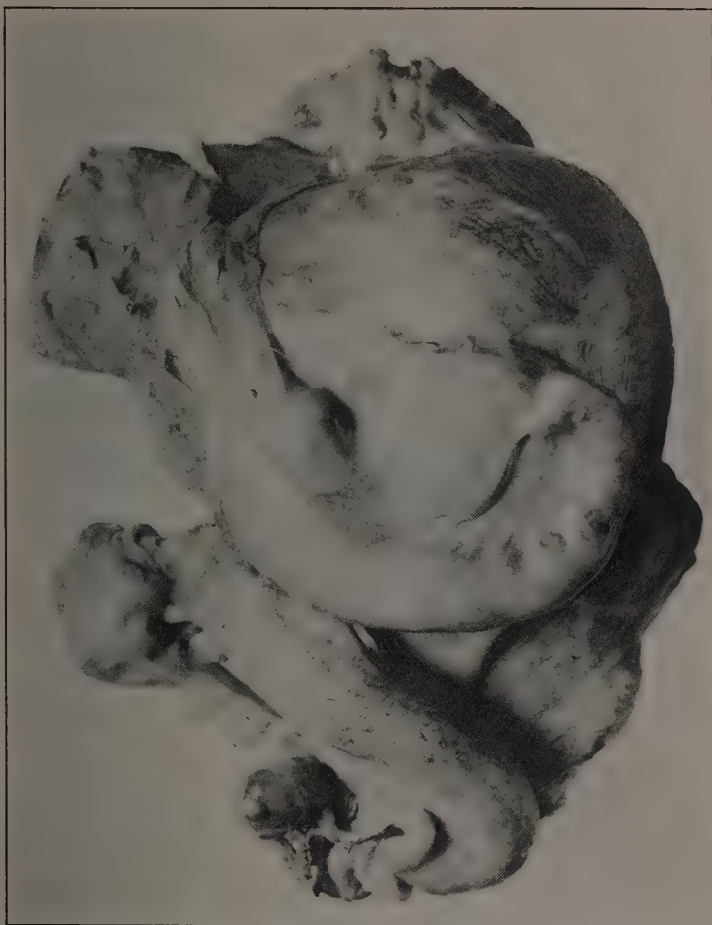
Fig. 21. Gross specimen, Genitalia, Case 4
Shows extensive periuterine abscesses.
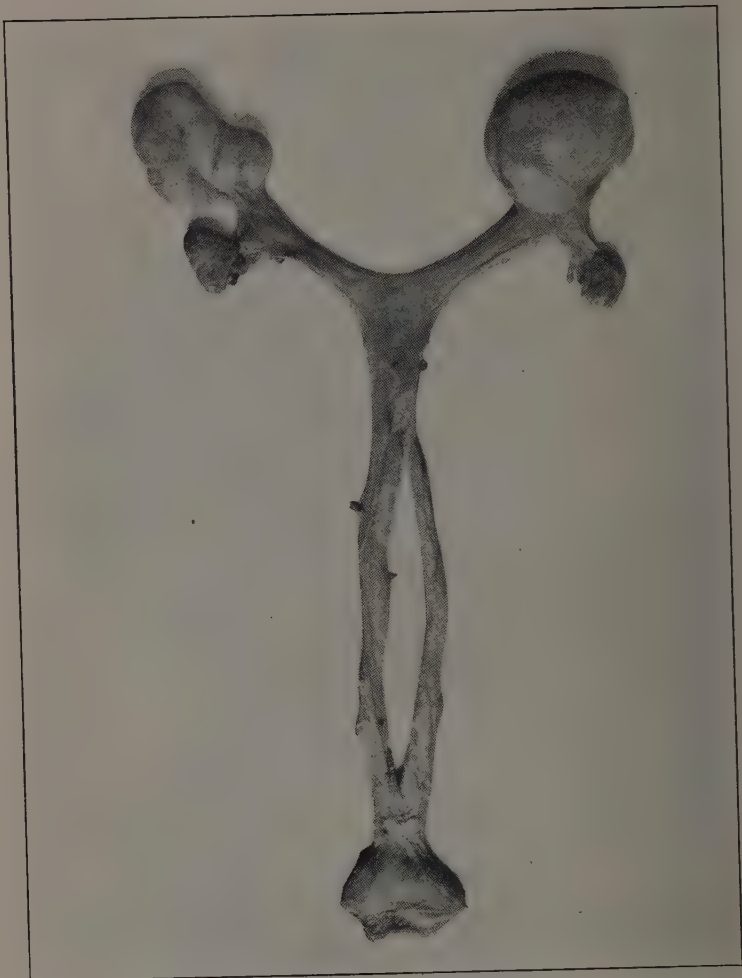
Fig. 22. Maldeveloped Genitalia, Case 13

The University of Minnesota
Agricultural Experiment Station

Comparison of First Generation
Tomato Crosses and Their Parents

By Richard Wellington
Division of Horticulture

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The University of Minnesota
Agricultural Experiment Station

Comparison of First Generation Tomato Crosses and Their Parents

By Richard Wellington
Division of Horticulture

CONTENTS

ILLUSTRATIONS

COMPARISON OF FIRST GENERATION TOMATO CROSSES AND THEIR PARENTS

By Richard Wellington[1]

INTRODUCTION

The crossing of closely related varieties of plants and animals is known to produce individuals which are larger and more vigorous and more prolific than either parent. However, little is known as to the frequency of their occurrence and their value in agricultural pursuits. In order to determine whether first generation tomato crosses were superior to their parents, and if so, whether certain crosses were more valuable than others, experiments were carried on from 1909 to 1919, inclusive, at University Farm, St. Paul.

REVIEW OF PREVIOUS STUDIES ON FIRST GENERATION TOMATO CROSSES

Hedrick and Booth (1907) noted that first generation hybrid tomatoes were much more vigorous and productive than their parent varieties and suggested that such crosses might have marketable value. The writer (1912) proved that this assumption was correct in the case of crosses between Dwarf Aristocrat and Hedrick and Stone.

East and Hayes (1912) reported that the cross between Golden Queen and Sutton's Best of All outyielded both parents.

Gilbert (1912) also noted that F_1 hybrids between a standard and a dwarf not only resembled the tall parent, but were a little taller and more vigorous.

Groth (1911), who made an extensive study of the size inheritance of F_1 generation tomato foliage, found that "Practically all characters studied tend to exceed the mean between the values of the parents, in the F_1 of the cross, so that the leaves of the cross tend to be longer, narrower, and possess a greater number of segments than the

mean between the values for the parents or even than either of the parents themselves. In other words, the crosses tend to be more vigorous than the parents." Later, in his report on the inheritance of size and shape of fruits (1912 and 1915), he states, "The size and shape of the F_1 crosses between $\pm$ round fruits are the geometric means of parental sizes and shapes."

Perry (1915) took issue with Groth and states that his explanation would be more tenable if the tomato fruits were perfect spheres, for irregularity of shape is liable to cause considerable error. He thought that the size of fruits could be better obtained from weights than from linear dimensions and in his investigations he found the size of the F_1 generation of the currant-pear cross to be the geometrical mean between the sizes of its parents. This phenomenon was thought to hold only when the fruit of the parents differed greatly in size, for when parents produced fruit of similar size, he thought their progeny would produce fruit approaching the arithmetical mean. As he based his opinions on weights obtained from a small number of plants, and only a portion of the fruit selected from each plant, his conclusions require further confirmation before final acceptance.

Hood (1915) noted seven F_1 standard $\times$ dwarf crosses which out-yielded their parents in weight and number of fruits. The standard plants of the F_2 and F_3 generations, however, yielded less fruit than those of the F_1 generation. Increased vigor and thriftiness were also noted in the crosses.

Von Tschermak (1916), in discussing tomato breeding investigations, mentioned that in 1914 at Eisgrub an F_1 generation cross between Ficarrazzi and Cooper's First Crop gave over 1 kg. of fruit per plant more than the parents. Other crosses gave no increase, or at least not in this amount. The explanation of the negative results was that they were probably due to the same causes noted by Shull and East in maize, that is, to the lack of heterozygous elements in the crosses.

Stuckey (1916) in his report on blossom-end rot investigation, stated that the first generation cross between Red Cherry and Greater Baltimore gave a higher yield of fruit than any of the fourteen varieties with which it was compared. From the figures given, this cross produced 48.52% more marketable fruit before June 30 than Earliana, the earliest of the varieties.

Hayes and Jones (1916) proved that "Continuous self-fertilization during periods of three and four years in four commercial varieties of tomatoes did not cause any significant decrease in the size or yield of fruit, but merely resulted in isolating, in the first year, types which varied either above or below the original unselected varieties in this

character," and further that "Vigor due to crossing as measured by increased yields was not appreciably greater in crosses between artificially selfed strains than in crosses between ordinary commercial varieties." These results were explained as due to the fact that the tomato is almost completely self-fertilized. In the crosses Stone × Dwarf Champion and Lorillard × Best of All there were obtained respectively 8 and 3% average increase in weight per fruit over the parental average. The Stone × Dwarf Champion cross also gave an 8% increase in the the average number of ripe fruits over the average of the parents, and approached the fruit number of the better parent, while the Lorillard × Best of All cross gave no increase.

Through four years the Stone × Dwarf Champion cross gave an increased yield, varying from 11 to 17% over the higher yielding parent. Lorillard × Best of All cross did not, on the other hand, exceed the better parent in yield, altho it did out-yield the average of the parents. The Stone × Dwarf Champion cross ripened its fruit earlier than the earlier parent, and thus the authors concluded that "hybrid vigor effects a result directly opposite to favorable environmental conditions which tend to delay maturity."

EXPERIMENTAL INVESTIGATIONS AND MATERIAL

The comparison of first generation tomato crosses at the Minnesota station was begun in 1909 by A. R. Kohler. Data collected during the first two years were preliminary in nature and are therefore not published; nevertheless they indicated the value of F_1 generation crosses and the advisability of continuing the experimental work on a more extensive and more exact scale. From 1911 to 1913, inclusive, a large number of F_1 crosses were tested, but as only seven plants of each cross were planted and no effort was made to grow the parents from self-fertilized seed or near their crosses, the data for each cross are not given. However, the average performance of all the crosses during each season has been calculated and is discussed under the next topic.

The most promising and unpromising crosses grown in 1913 were selected by R. C. Rose for testing in 1914. Seed of the varieties and crosses was produced during the winter in the greenhouse. About June 1 three rows of thirty plants each of the F_1 crosses and their parents were set out. Wherever possible the F_1 plants and their parents were planted in contiguous rows. Similar methods of procedure in securing seed and planting were followed from 1915 to 1919, except that most of the crosses and selfed plants were produced from

known individuals and that fewer plants were grown, about twenty-five of each cross and parent being grown from 1915 to 1918 and six in 1919.

The method of growing the plants each year was similar to that practiced by many commercial growers in the northern states, that is, the seed was sown about the first week in April in flats in the greenhouse, and when the seedlings began to develop their true leaves, they were potted in two-inch pots. Later the plants were transferred to four-inch pots and after danger of frost, about May 30, were set in the field. A guard row was always planted around the entire field in order to give each plant the same amount of space, 5 by 5 feet.

PRELIMINARY WORK FROM 1911 TO 1913, INCLUSIVE

From 1911 to 1913, inclusive, 130 first-generation tomato crosses were grown and compared with their parents, but for reasons already stated the performance of each individual cross is not given. The results obtained during this period are given in Table I.

TABLE I

COMPARISON OF YIELDS OF F_1 GENERATION CROSSES AND THEIR PARENTS, 1911-1913, INCLUSIVE

Year	No. of crosses tested		Average yield per plant of parents, lbs.		Average yield per plant of F_1 crosses, lbs.		Per cent increase in yield of F_1 crosses over average yield of parents		
	$D.\times S.$*	$S.\times S.$	D.	S.	$D.\times S.$	$S.\times S.$	$D.\times S.$	$S.\times S.$	All crosses
1911	19	..	6.39	13.44	16.24	....	63.63	....	63.63
1912	18	13	6.81	12.04	18.75	20.77	98.83	95.49	97.43
1913	18	62	13.95	26.24	31.21	31.03	44.13	11.57	18.89

*D=Dwarf.   S=Standard.

DISCUSSION OF TABLE I

In 1911 all the crosses were between dwarf and standard varieties, while in 1912 and 1913 part of the crosses were between dwarfs and standards, and part between standards and standards. Since the dwarfs yielded about half as much fruit as the standards and the first generation cross between dwarfs and standards yielded approximately the same as crosses between standards and standards, the increase in yield of first generation crosses between dwarf and standard varieties over the average yield of their parents was greater than that of crosses between standard varieties over the average yield of their parents. The data obtained in 1912 and 1913 which substantiate this statement are as follows: The percentage increase in 1912 of dwarfs × standards over the average yield of their parents was 98.83%, and

of standards $\times$ standards, 95.49%; and in 1913, 44.13% and 11.57%, respectively. The total percentage increase of all crosses over the average yield of their parents was 63.63% in 1911, 97.43% in 1912, and 78.89% in 1913.

INFLUENCE OF CROSSING UPON EARLINESS, NUMBER OF FRUITS, SIZE OF FRUITS, AND TOTAL PRODUCTION

From 1914 to 1919, inclusive, 60 first generation tomato crosses were compared with their parents. These crosses were derived from 14 varietal combinations. The number of times each variety was used in the crosses is as follows: Earliana 24, Bonny Best 16, Chalk Early Jewel 14, Stone 13, Beauty 10, My Maryland 10, June Pink 9, Dwarf Aristocrat 6, John Baer 5, Globe 5, Comet 4, Dwarf Champion 2, Buck Tresco and New Globe 1 each.

In 1914 the fruit was weighed but not counted, while in 1915, 1916, 1917, 1918, and 1919 it was both weighed and counted. The date of each picking was recorded, hence it has been possible to divide the crop into early, midseason, and late, and thus determine the effect of crossing upon earliness.

PERCENTAGE OF TOTAL NUMBER OF FRUITS RIPENED PER PLANT OF THE F_1 CROSSES AND THEIR PARENTS
(See first section of Table II.)

In order to determine whether the F_1 crosses ripened a greater proportion of their fruits than their parents, the percentage of the total number of fruits which ripened per plant was calculated. The crosses on the average did not ripen as many fruits as the higher parent, for only 21 out of the 60 surpassed the higher parent. The results obtained each season are as follows: In 1914, 4 out of 13 crosses ripened a greater proportion of their fruit than the higher parent; in 1915, 7 out of 24 surpassed the higher parent; in 1916, none of the crosses surpassed the higher parent; in 1917, 7 of the 9 crosses ripened a greater proportion of their fruit than the higher parent; while in 1918, 1 out of 4, and in 1919, 2 out of 3 ripened a greater proportion of their fruit than the higher parent.

PERCENTAGE INCREASE IN NUMBER OF RIPE AND GREEN FRUITS PRO-DUCED BY FIRST-GENERATION PLANTS OVER MEAN OF PARENTS AND HIGHER PARENT
(See second section of Table II.)

Crossing of varieties, however, caused a definite increase in the number of fruits produced, that is, when measurement is based upon mean of parents. In 1915, 17 out of 24 of the crosses produced more fruits than the mean of their parents; while in 1916, 1917, 1918, and 1919 the proportions were 7 to 7, 6 to 9, 4 to 4, and 2 to 3, respectively.

TABLE II

INFLUENCE OF CROSSING UPON EARLINESS, NUMBER AND SIZE OF FRUITS, AND TOTAL PRODUCTION

Cross	Percentage of total number of fruits ripened per plant			Percentage increase in number of ripe and green fruits produced by F₁ plant over		Percentage increase in size of individual ripe fruits of F₁ plants over		Percentage increase in total productivity by weight of F₁ plants over	
	Female	Male	F_1	Mean of parents	Higher parent	Mean of parents	Higher parent	Mean of parents	Higher parent
1914									
Beauty × Chalk Early Jewel*	82.7	86.6	88.7	...	...	...	...	19.2	12.1
Beauty × June Pink	82.7	97.4	93.8	...	...	...	...	29.7	15.5
June Pink × Beauty	97.4	82.7	97.5	...	...	...	...	33.0	17.6
Bonny Best × Globe	89.7	66.4	82.3	...	...	...	...	31.6	16.5
Chalk Early Jewel × Earliana	86.6	97.1	96.6	...	...	...	...	28.0	21.7
Earliana × Chalk Early Jewel	97.1	86.6	97.3	...	...	...	...	8.5	7.6
Chalk Early Jewel × Stone	86.6	60.6	78.8	...	...	...	...	14.8	1.4
Dwarf Aristocrat × Earliana	66.5	97.1	91.2	...	...	...	...	99.6	25.1
Dwarf Champion × Stone	68.8	60.6	67.0	...	...	...	...	44.3	3.5
Earliana × Dwarf Champion	97.1	68.8	96.0	...	...	...	...	83.0	18.3
Earliana × My Maryland	97.1	62.2	94.8	...	...	...	...	30.7	15.7
My Maryland × Bonny Best	62.2	89.7	83.7	...	...	...	...	-0.7	-16.0
My Maryland × Globe	62.2	66.4	79.7	...	...	...	...	38.0	9.6
1915									
Beauty × Chalk Early Jewel†	26.0	24.1	26.8	4.6	-1.3	9.4	-1.2	13.5	4.1
Chalk Early Jewel × Beauty	24.1	26.0	33.1	-7.4	-11.4	-3.8	-15.0	4.1	-4.6
Beauty × Earliana	20.7	73.2	71.0	11.4	-5.6	-13.5	-32.8	0.9	-35.8
Beauty × June Pink	32.4	21.5	24.1	-19.7	-27.2	8.2	4.6	-5.4	-11.1
Beauty × My Maryland	16.4	20.1	21.5	-2.3	-16.0	9.6	-13.6	16.3	13.4
Bonny Best × June Pink	65.6	74.9	84.9	28.1	24.7	-22.8	-45.4	5.9	-6.1
Bonny Best × My Maryland	56.8	16.9	34.2	21.6	-1.8	16.3	1.8	32.2	6.8

Bonny Best × Stone	67.9	17.5	42.2	4.1	—6.8	—8.2	—75.2	9.3	—10.5
Stone × Bonny Best	17.5	67.9	31.0	13.1	0.2	—3.2	—18.8	12.0	—7.9
Chalk Early Jewel × Bonny Best	21.7	76.7	49.3	12.6	4.4	12.7	1.8	19.0	10.7
Chalk Early Jewel × Earliana	24.6	71.3	70.1	31.5	11.8	—6.1	—6.9	24.7	—2.0
Chalk Early Jewel × June Pink	29.3	21.5	32.1	—4.1	—9.8	7.5	0.7	6.5	1.9
Chalk Early Jewel × My Maryland	22.4	14.9	15.9	—0.4	—12.0	1.3	—5.6	—0.1	—7.3
Dwarf Aristocrat × Stone	20.8	17.5	17.7	19.8	8.6	3.7	—26.9	53.1	23.5
Dwarf Aristocrat × Bonny Best	34.0	83.4	56.8	64.6	30.2	21.0	5.9	79.9	25.6
Earliana × Dwarf Aristocrat	71.3	29.4	65.4	89.6	56.5	—8.3	—25.6	74.8	13.8
Earliana × Globe	65.0	16.2	68.2	—5.6	—9.2	18.7	52.2	—4.1	—10.2
Earliana × My Maryland	80.0	20.1	58.5	30.3	10.8	—17.8	—50.6	26.5	4.3
Globe × Dwarf Aristocrat	25.6	33.0	39.9	55.6	15.0	3.1	—24.3	75.9	15.9
My Maryland × Dwarf Aristocrat	17.0	26.3	17.9	52.5	28.7	4.3	—23.0	73.3	24.3
Stone × Beauty	20.4	70.0	60.7	49.8	14.5	15.5	—39.2	44.6	6.2
Stone × Earliana	30.4	86.4	76.7	56.0	23.8	—21.9	—42.2	31.0	5.5
Stone × June Pink	19.4	74.9	59.0	61.6	26.8	—17.0	—40.3	49.6	15.1
Stone × My Maryland	—21.4	39.2	30.2	—20.5	—25.0	1.3	2.6	—18.9	—48.2
1916									
Bonny Best × Earliana†	51.3	76.4	55.9	40.6	32.2	—14.0	—31.3	15.0	8.2
Bonny Best × June Pink	45.4	70.8	54.9	54.5	39.8	—27.1	—55.2	12.8	8.5
Chalk Early Jewel × Bonny Best	37.9	48.0	38.9	14.7	2.4	9.2	3.6	10.6	—0.1
Chalk Early Jewel × Earliana	27.2	63.9	48.4	59.8	59.4	—16.3	—27.0	37.3	20.5
John Baer × Earliana	51.9	76.4	59.9	58.8	63.8	—27.6	—49.7	13.3	11.3
Stone × Earliana	28.3	71.8	49.2	99.4	77.9	—24.2	—37.9	44.3	14.9
Stone × June Pink	11.1	70.8	43.5	73.4	51.8	—19.8	—42.8	43.8	11.2
1917									
Bonny Best × Cornett†	62.6	46.4	54.8	19.9	7.6	0.0	—12.7	19.3	13.9
Bonny Best × Earliana	77.4	57.4	87.2	—7.2	—23.5	—13.6	—17.0	—8.5	—20.5
Bonny Best × Earliana	61.3	57.4	94.3	5.2	—15.0	—26.8	—43.5	—3.5	18.1
Buck Tresco × Earliana	14.6	54.2	67.1	50.7	31.0	—17.4	—59.4	55.0	24.0

TABLE II—Continued

INFLUENCE OF CROSSING UPON EARLINESS, NUMBER AND SIZE OF FRUITS, AND TOTAL PRODUCTION

Cross	Percentage of total number of fruits ripened per plant			Percentage increase in number of ripe and green fruits produced by F₁ plant over		Percentage increase in size of individual ripe fruits of F₁ plants over		Percentage increase in total productivity by weight of F₁ plants over	
	Female	Male	F₁	Mean of parents	Higher parent	Mean of parents	Higher parent	Mean of parents	Higher parent
Comet × Earliana	40.8	67.5	71.4	21.5	−2.6	−17.5	−45.5	4.2	−0.3
Globe × Comet	53.1	34.4	56.6	22.8	−16.5	−13.6	−61.2	29.4	19.7
John Baer × Earliana	71.2	70.4	91.7	23.6	−4.2	−17.7	−68.0	9.7	0.2
John Baer × Earliana	77.4	70.4	88.5	0.0	−10.6	−17.3	−42.9	−0.5	−0.7
John Baer × Comet	84.2	30.4	69.5	−6.4	−71.4	−8.4	−37.6	−3.3	−7.9
1918									
My Maryland × June Pink†	16.8	66.3	41.2	51.8	24.2	−1.9	−3.4	46.8	20.8
Beauty × Stone	58.7	12.4	32.6	62.2	41.9	−1.0	−11.1	47.3	29.3
Chalk Early Jewel × Stone	35.1	14.6	23.9	13.9	−11.5	6.4	3.0	22.7	0.1
John Baer × Earliana	35.7	45.7	58.7	11.9	12.1	−29.1	−38.4	3.7	4.5
1919									
Bonny Best × Chalk Early Jewel‡	76.5	82.2	86.5	−12.3	−38.1	20.8	9.2	12.5	1.7
Bonny Best × Earliana	94.0	96.0	96.6	17.6	13.8	−16.7	−33.3	−0.1	−6.9
New Globe × Earliana	36.8	96.0	81.4	22.2	−2.7	−26.4	−52.1	1.5	−17.7

* Thirty plants each of the F₁ plants and their parents were set out.
† Twenty-five plants each of the F₁ plants and their parents were set out.
‡ Data taken on 6 plants of the F₁ plants and their parents.

The increase over the higher parent was less consistent, altho over half the crosses produced more fruits than the higher parent. The proportion of the crosses which have produced more fruit than the higher parent for the respective years is as follows: 1915, 13 to 24; 1916, 7 to 7; 1917, 2 to 9; 1918, 3 to 4; and 1919, 1 to 3.

PERCENTAGE INCREASE IN SIZE OF INDIVIDUAL RIPE FRUITS OF F_1 PLANTS OVER MEAN OF PARENTS AND HIGHER PARENT

(See third section of Table II.)

As would naturally be expected the increase in number of fruits per plant caused a decrease in size of the ripe fruit. This decrease in size was most marked in those years when the increase in number of fruits was the greatest, namely 1916 and 1917. The proportion of crosses which gave a higher percentage increase in size of ripe fruits over the mean of parents for the years 1915 to 1919, inclusive, was respectively as follows: 14 to 24, 1 to 7, 0 to 9, 1 to 4, and 1 to 3. With the exception of 1915, these proportions held when the crosses were compared with the higher parent.

PERCENTAGE INCREASE IN TOTAL PRODUCTION OF RIPE AND GREEN FRUITS BY WEIGHT OF F_1 PLANTS OVER MEAN OF PARENTS AND HIGHER PARENT

(See fourth section of Table II.)

The increase in productivity of F_1 crosses over their parents has been marked during the whole experiment. In 1914, 12 of the 14 crosses gave more fruit than the mean of their parents and the higher yielding parent; in 1915, 20 of the 24 crosses gave more fruit than the mean and 14 more than the higher parent; in 1916, all 7 crosses produced more fruit than the mean and 6 more than the higher parent; in 1917, 5 of the 9 crosses gave more fruit than both the mean of parents and higher parent; in 1918, all the crosses outyielded the parental mean and higher parent; while in 1919, 2 outyielded the mean of the parents and 1 the higher parent. The percentage of increase for the same cross has fluctuated more or less during different seasons and within the same season. For example, Chalk Early Jewel × Earliana gave increases over the mean of parents and higher parent of 28.0% and 21.7%, respectively, in 1914; of 24.7% and —2.0% in 1915; and 37.3% and 20.5% in 1916; while the reciprocal cross gave increases of 8.5% and 7.6% in 1914. Again, John Baer × Earliana gave increases of 13.3% and 11.3% in 1916; 9.7%, and 0.2%, and —0.5% and —0.7% in 1917; and 3.7% and 4.5% in 1918. These variations may have been partly due to a difference in varietal strains used in the production of the crosses and partly to experimental error that is bound to occur in field experiments. It is evident that the merit of a first generation cross must be determined by its performance over a series of years.

BEAUTY X CHALK
EARLY JEWELL

CHALK EARLY
JEWELL X BEAUTY

BEAUTY X
EARLIANA

BEAUTY X
JUNE PINK

BEAUTY X
MY MARYLAND

BONNY BEST X
JUNE PINK

BONNY BEST X
MY MARYLAND

BONNY BEST
X STONE

STONE X
BONNY BEST

CHALK E. JEWELL
X BONNY BEST

CHALK E. JEWELL
X EARLIANA

CHALK E. JEWELL
X JUNE PINK

CHALK E. JEWELL
X MY MARYLAND

DWARF ARISTOCRAT
X BONNY BEST

DWARF ARISTOCRAT
X STONE

EARLIANA X
DWARF ARISTOCRAT

EARLIANA X
GLOBE

EARLIANA X
MY MARYLAND

GLOBE X
DWARF ARISTOCRAT

MY MARYLAND X
DWARF ARISTOCRAT

STONE X BEAUTY

STONE X
EARLIANA

STONE X
JUNE PINK

STONE X
MY MARYLAND

1915

EARLIANA

BONNY BEST
X JUNE PINK

CHALK E. JEWELL
X EARLIANA

CHALK E. JEWELL
X BONNY BEST

JOHN BAER X
EARLIANA

1916

STONE X
EARLIANA

STONE X
JUNE PINK

BONNY BEST
X COMET

BONNY BEST
X EARLIANA

BONNY BEST
X EARLIANA

1917

BUCK TRESCO
X EARLIANA

COMET X
EARLIANA

GLOBE X
COMET

JOHN BAER
X EARLIANA

JOHN BAER
X EARLIANA

JOHN BAER
X COMET

MY MARYLAND
X JUNE PINK

BEAUTY
X STONE

1918

CHALK E. JEWELL
X STONE

JOHN BAER
X EARLIANA

BONNY BEST X
CHALK E. JEWELL

BONNY BEST
X EARLIANA

NEW GLOBE
X EARLIANA

Fig. 1. Number of Ripe and Green Fruits Produced per Plant by Means of Parents, Higher Yielding Parents, and F₁ Cross
The fruits ripening in the early part of the season are designated by a solid marking, in midseason by cross-hatching, in late season by stippling, and green fruits by blank bars. The upper line of each cross represents the mean of the parents, the middle line the higher yielding parents, and the lower line the first-generation cross. It is readily seen that the first-generation crosses having Earliana or its close relative, June Pink, for one parent, have made the most marked increase over the mean of the parents and the higher yielding parent.
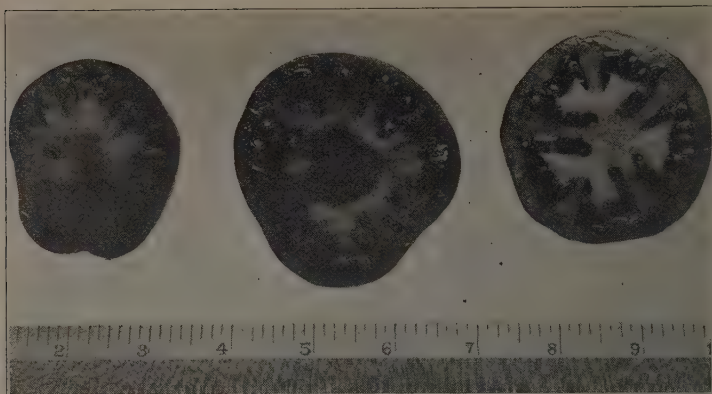
Fig. 2.   Fruit of Earliana

Few or no seed in cells of the two Earliana fruits to the left are correlated with their irregular shape.

INFLUENCE OF CROSSING UPON EARLINESS AS INDICATED BY INCREASE IN PRODUCTION OF RIPE FRUIT

(Calculated in pounds per acre for early, midseason, and late season varieties.)

In order to determine the effect of crossing upon earliness, as the crosses seemed often to ripen earlier than either parent, the season was divided into three parts: early, midseason, and late, and the crop was calculated separately for each part. (See Table III.) The data are arranged in two main sections in order to show (1) the increased yield over the mean of parents and (2) the increased yield over the higher parent. The second section is of particular interest to the grower, for if the cross is less productive than the higher parent its value is nil, that is, from the yield standpoint. Yield, however, is not the only character of a commercial fruit. Smoothness is also a desirable character of first generation crosses, as is indicated later.

Fig. 3.   Stone Tomato—Fruit Firm and Regular
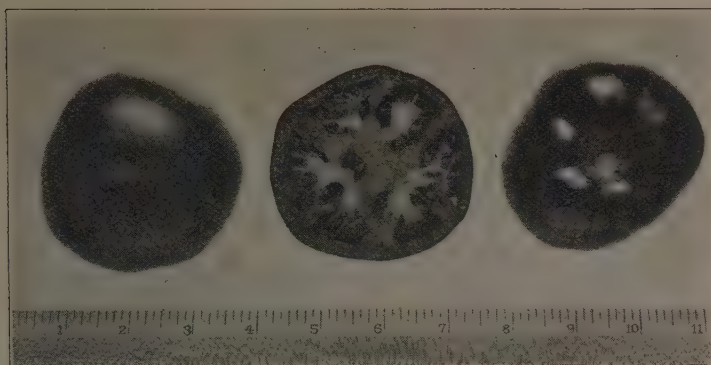
Fig. 4. Stone × June Pink F₁
The fruit is firmer and more regular than the male parent.

In 1915, the crosses ripened more fruit than the mean of the parents in the following proportions: 14 to 20 in early season, 17 to 24 in midseason, 19 to 24 in late season, and 18 to 24 in the total season. In 1916, the proportions for the same respective seasons were 5 to 6, 6 to 7, 5 to 7, and 7 to 7. In 1917, the proportions were 8 to 9, 9 to 9, 7 to 9, and 9 to 9. In 1918, the proportions were 3 to 4, 4 to 4, 3 to 4, and 4 to 4; while in 1919 the proportions were 3 to 3, 2 to 3, 2 to 3, and 3 to 3. Summarizing the performance of the crosses for the five years, we find 33 gave an increase and 9 a decrease in the early part of the season, 38 an increase and 9 a decrease in midseason, 36 an increase and 11 a decrease in late season, and 41 an increase and 6 a decrease in the season as a whole. The evidence thus strongly supports the statement that crossing tomatoes hastens the maturity of the fruit.

Fig. 5. June Pink—Fruit Soft and Irregular

TABLE III

INFLUENCE OF CROSSING UPON EARLINESS AS INDICATED BY INCREASE IN PRODUCTION OF RIPE FRUIT, CALCULATED IN POUNDS PER ACRE FOR EARLY, MID-SEASON, AND LATE

Cross	Increase in pounds per acre of F_1 plants over mean yield of parents				Increase in pounds per acre of F_1 plants over yield of higher parent			
	Early	Mid-season	Late	Total	Early	Mid-season	Late	Total
1915								
Beauty × Chalk Early Jewel	—17.4	.348.5	906.1	1,237.1	17.4	60.7	871.2	958.3
Chalk Early Jewel × Beauty	87.1	1,568.2	505.3	2,160.6	122.0	1,289.4	470.5	1,881.8
Beauty × Earliana	731.8	1,324.2	4,024.9	5,993.9	—69.7	—2,387.1	—9,199.9	—11,656.7
Beauty × June Pink	—156.8	—209.1	—453.0	—818.9	—226.5	—453.0	—1,324.2	—2,003.8
Beauty × My Maryland	0 0	383.3	1,533.3	1,916.6	—17.4	278.8	1,132.6	1,393.9
Bonny Best × June Pink	1,951.5	5,453.7	—331.1	7,074.1	1,590.1	3,850.7	—3,362.8	2,178.0
Bonny Best × My Maryland	87.1	—522.7	1,603.0	1,167.4	156.8	—1,725.0	—5,854.5	—7,736.3
Bonny Best × Stone	—104.5	—592.4	156.8	—540.1	—522.7	—2,317.3	—7,684.0	—10,524.1
Stone × Bonny Best	—191.7	—1,341.7	—2,334.8	—3,868.1	—609.8	—3,066.6	—10,175.6	—13,852.1
Chalk Early Jewel × Bonny Best	—122.0	296.2	2,596.2	3,014.4	—87.1	—1,237.1	—2,247.7	—3,571.9
Chalk Early Jewel × Earliana	993.2	2,909.8	9,252.1	13,155.1	331.1	—1,254.5	—383.3	—1,306.8
Chalk Early Jewel × June Pink	0.0	1,515.9	906.1	—2,421.9	—69.7	1,272.0	—191.7	1,010.6
Chalk Early Jewel × My Maryland	0.0	—261.4	—453.0	—714.4	0.0	—557.6	—1,428.8	—1,986.3
Dwarf Aristocrat × Bonny Best	122.0	—139.4	5,384.0	5,366.6	—52.3	2,700.7	1,341.7	—1,411.3
Dwarf Aristocrat × Stone	52.3	156.8	1,411.3	1,620.4	69.7	87.1	1,150 0	1,306.8
Earliana × Dwarf Aristocrat	801.5	1,637.9	13,311.9	15,751.3	52.3	—1,846.9	3,781 0	1,986.3
Earliana × Stone	644.7	3,903.0	7,143.8	11,891.5	278.8	1,080.3	479.5	1,829.5
Earliana × My Maryland	0.0	—1,289.4	7,544.6	6,255.2	—784.1	—5,889.3	1,446.2	—5,227.2
Globe × Dwarf Aristocrat	278.8	1,272.0	5,540.8	7,091.6	296.2	1,132.6	3,937.8	5,366.6
My Maryland × Dwarf Aristocrat	87.1	52.3	1,986.3	2,125.7	104.5	87.1	1,533.2	1,725.0
Stone × Beauty	418.2	1,446.2	8,834.0	10,698.3	—278.8	—2,387.1	435.6	—2,230.3
Stone × Earliana	487.9	2,875.0	6,377.2	9,740.0	—836.4	—2,178.0	1,219.7	—17,994.7
Stone × June Pink	296.2	1,097.7	9,600.6	10,994.5	—662.1	—2,526.5	975.7	—2,212.9
Stone × My Maryland	—32.9	17.4	—2,300.0	—2,317.4	—87.1	—453.0	—6,046.1	—6,586.3

1916								
Bonny Best × Earliana*	−32.9	−52.3	2,369.7	2,282.5	−871.2	−3,101.5	1,585.6	−2,387.1
Bonny Best × June Pink	714.4	2,543.9	−243.9	3,014.4	714.4	1,167.4	−3,641.6	−1,759.8
Chalk-Early Jewel × Bonny Best	0.0	679.5	2,097.0	3,676.5	17.4	−1,080.3	3,206.0	2,143.2
Chalk Early Jewel × Earliana	331.1	5,837.0	4,547.7	10,715.8	34.9	4,164.3	−1,899.2	2,300.0
John Baer × Earliana	1,167.4	4,512.8	−2,770.4	2,909.1	278.8	4,042.4	−4,180.8	139.4
Stone × Earliana	505.3	5,262.1	4,512.8	10,280.2	17.4	1,515.9	−2,543.9	−1,010.6
Stone × June Pink	313.6	2,073.5	8,415.8	10,802.9	−139.4	−2,491.6	−418.2	−3,049.2
1917								
Bonny Best × Comet*	34.9	139.4	3,397.7	3,624.6	−122.0	−209.1	1,341.7	1,010.6
Bonny Best × Earliana	749.2	540.1	−522.7	766.7	697.0	17.4	−906.1	−191.7
Bonny Best × Earliana	731.8	1,533.3	1,968.9	4,303.7	883.7	836.4	191.7	1,916.6
Buck Tresco × Earliana	1,045.4	1,446.2	10,419.6	12,911.2	836.4	383.3	5,610.5	6,830.2
Comet × Earliana	697.0	1,846.9	2,857.5	3,669.0	662.1	1,010.6	453.0	2,125.7
Globe × Comet	435.6	1,115.1	6,725.7	8,276.4	453.0	697.0	4,077.2	5,227.2
John Baer × Earliana	697.0	2,896.1	2,090.9	5,593.1	505.3	2,474.2	1,463.6	4,443.1
John Baer × Earliana	958.3	2,265.1	−348.5	2,975.0	1,010.6	2,265.1	−1,550.7	1,725.0
John Baer × Comet	−139.4	784.1	4,669.6	5,314.3	−435.6	278.8	1,202.3	1,045.4
1918								
My Maryland × June Pink*	104.5	2,143.2	6,185.5	8,433.2	−1,184.8	−17.4	3,571.9	2,359.7
Beauty × Stone	87.1	765.7	6,063.6	6,017.3	−1,289.4	1,498.5	1,585.6	−1,202.3
Chalk Early Jewel × Stone	243.9	1,637.9	−1,028.0	853.8	−679.5	−975.7	−5,349.2	−7,004.5
John Baer × Earliana	−209.1	122.0	5,959.0	5,871.9	−557.6	−400.8	5,784.8	4,826.5
1919								
Bonny Best × Chalk Early Jewel†	2,968.9	2,125.7	3,484.8	8,102.2	2,753.0	383.3	1,184.8	4,321.2
Bonny Best × Earliana	5,401.4	−993.7	−4,199.2	209.1	903.2	−5,227.2	975.7	−3,432.5
New Globe × Earliana	209.1	3,223.4	8,119.6	11,552.1	−6,115.8	−5,540.8	18,521.7	6,865.1

*Twenty-five plants each of the F_1 plants and their parents were set out.

†Data taken on 6 plants each of the F_1 plants and their parents.

In summarizing the performance of the crosses as compared with the higher yielding parent, a positive increase is found, altho its margin is small. During the five years, 24 crosses gave an increased yield and 22 a decreased yield in the early part of the season, 24 an increased and 23 a decreased yield in midseason, 28 an increased and 19 a decreased yield in late season, and 25 an increased and 22 a decreased yield in the entire season.

EFFECT OF CROSSING ON SMOOTHNESS OF FRUITS

In 1914, 1915, 1916, 1917, and 1918, the fruit when picked was graded into No. 1 and No. 2, according to smoothness, size, and condition. Invariably the first generation crosses made between rough types, as Earliana and June Pink; and smooth types, as Bonny Best and Chalk Early Jewel, were found to have a much higher percentage of first-grade fruit than the rough parent; or, in other words, the smooth surface of one parent dominated to a high degree the rough surface of the other. In 1916, a dry hot season, a large number of smooth fruits were thrown out of grade 1 on account of their small size, and since the F_1 crosses produced proportionately more small fruits than their parents, the percentage of grade 1 fruit in that season is not an accurate index of smoothness.

The cause of the increased smoothness has not been determined, but it seems probable that the surface character, like the size character, is dependent upon numerous factors and therefore is inherited apparently as an intermediate character. The assumption is further supported by the fact that no simple splitting of smoothness of fruit surface occurs in the second generation. Roughness may be accentuated by excessive moisture, type of soil, and imperfect fertilization of the ovules. At least the shrunken areas of rough fruits like those of Earliana are frequently deficient in seed (see Fig. 1) and certain regions produce rough types of Earlianas. The cause of the irregularity often arises earlier than the fertilization stage, as the ovary previous to fertilization may be markedly irregular. Strange to say, no tomato with smooth fruit, except first generation crosses, ripens its fruit as early as Earliana—a bearer of more or less irregular fruits.

RELATION OF CLIMATIC CONDITIONS TO NUMBER AND SIZE OF FRUITS

EFFECT OF WEATHER ON YIELD

The variations in the yield of fruit which occurred during eight years of investigation must have been due largely to the variations in climatic conditions, since the soil type, and amount of manure applied was fairly uniform each year. In Figure 6 is shown the relation of the average yield per plant of the standard varieties for each season to the mean rainfall and temperature of the growing months, namely, June, July, August, and September. The maximum yield was obtained in 1913 when the plants received sufficient moisture and heat during the months of June and July to produce an optimum growth, and sufficient dry weather and heat during August to cause the setting and ripening of a large number of fruits. The mean temperature for June and July, 1913, was 70° and 69.9° F. and of August and September 72.2° and 60.8° F., respectively, while the rainfall of these months was 3.05, 6.11, 1.59, and 3.34 inches, respectively. In 1916, when the second highest yield of the varieties was obtained, the mean temperature of June, July, August, and September was respectively, 63°, 76.6°, 70.4°, and 58.4°, and the rainfall 1.0, 0.72, 1.57, and 2.33 inches. Abnormally low rainfall throughout the season must have reduced the yield, and the low mean temperature of June must have checked the growth of the plants.
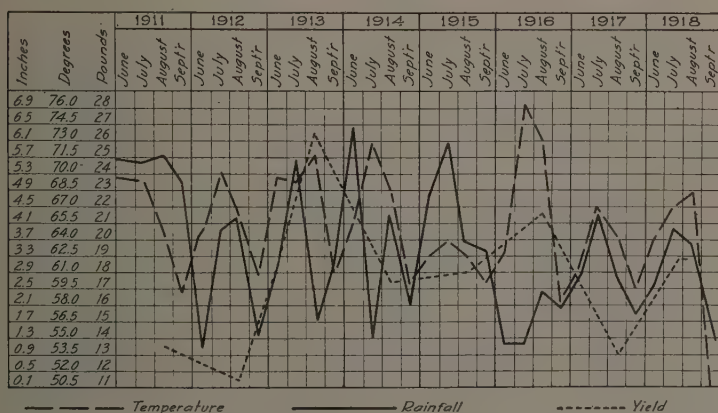
Fig. 6.   Average Temperature and Rainfall, and Average Yield of Varieties per Plant for the Growing Months, June, July, August, and September
Note relation of temperature and rainfall to yield.

In 1911, 1912, 1914, 1915, and 1917, when the yields were comparatively low, the mean temperature, particularly during August, was uniformly low. The yield in 1914 was also probably affected by the drouth in July which checked the growth of the plants. The cause of high and low yields each year can thus be explained satisfactorily by the amount of rainfall and the temperature during the months of June, July, August, and September. In other words, a maximum tomato crop is dependent upon sufficient moisture and heat to produce large vigorous plants, and sufficient dry weather and heat after the plant has reached its critical period (the time of setting first fruits) to cause the setting and development of a large number of fruits.
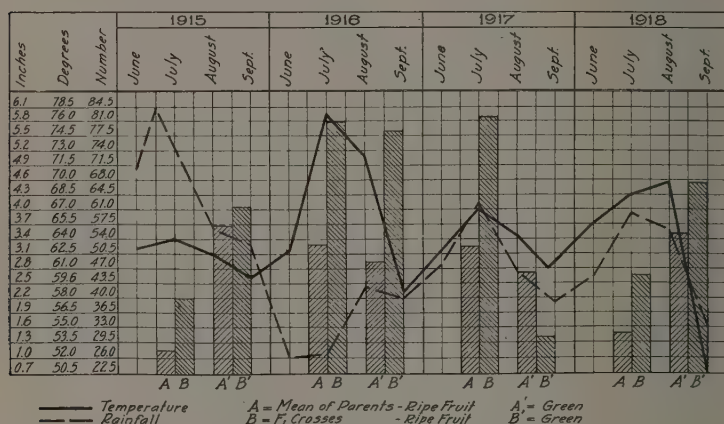
Fig. 7. Amount of Rainfall, Average Temperature, and Average Yield per Plant by the F₁ Generation Crosses and Their Parents

Note (1) that the crosses produced more ripe fruits in 1916 and 1917, when the mean temperature was greater, and (2) that most fruit set in 1916 when the temperature was high and the rainfall was low in the early part of the season.

A curious reversal in yield took place in 1915 and 1916. The low and high-yielding strains of Bonny Best, Chalk Early Jewel, Earliana, and Stone grown in 1915 reversed their positions the following year. As the soil conditions were similar, the variations must have been due to climatic conditions, as 1915 was a cold wet season and 1916 a hot dry one. If this assumption is correct, then the conclusion may be drawn that certain strains are better adapted to certain climatic conditions than others and further that one-year tests of strains are of value only for that particular season.

EFFECT OF SEASONAL CONDITIONS ON NUMBER OF RIPE AND GREEN FRUITS PRODUCED, 1915 TO 1918, INCLUSIVE, BY F₁ CROSSES AND THEIR PARENTAL MEANS

The number of fruits and the proportion of ripe and green fruits produced by the F_1 crosses and the mean of their parents fluctuated markedly during the years 1915 to 1918, inclusive. Figure 7 shows these variations as correlated with rainfall and temperature. Undoubtedly wide variation also occurred during the seasons from 1911 to 1914, but no data were taken in these years on the number of fruits.

The low average number of ripe fruits produced in 1915 and 1918 was undoubtedly due to cold weather. In 1915 the cool weather was fairly uniform throughout the season, while in 1918 it occurred during August and September when the fruits should have been ripening. In 1916 and 1917 the temperature averaged higher throughout the season and the number of ripe fruits was markedly greater. The green fruits, however, were much more numerous in 1916 than in 1917. This variation might have been due to the high temperature and low rainfall in the early part of 1916, which caused an extra heavy setting of fruit.

EFFECT OF RAINFALL ON SIZE OF FRUITS

In 1916 the rainfall was exceptionally low, and as it came mainly at distinct periods it was easy to determine its effect on the size of fruits. To illustrate this effect, which was similar in all varieties and crosses, Earliana, Stone, and their F_1 cross were selected. (See Fig.
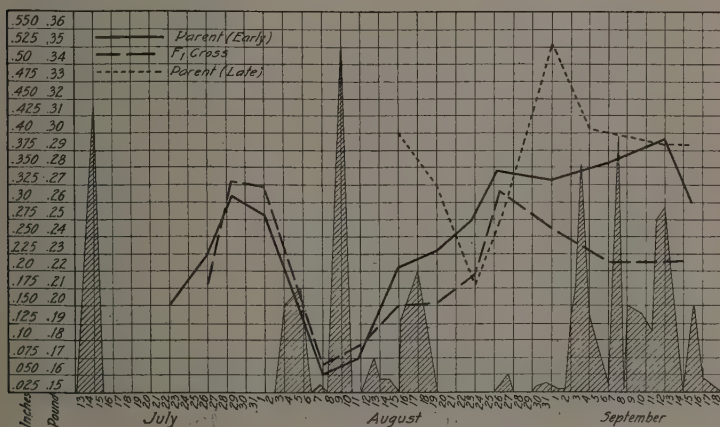
Fig. 8. Amount of Rainfall, Time of Occurrence, and Average Size of Fruits of Earliana, Stone, and Their First-Generation Cross

Note the length of time required after each rainfall for the fruits to reach their maximum size. The decrease in size could have been prevented by irrigating about every two weeks.

8.)   On July 2 and 3 the rainfall recorded was 0.2 inch, and no more rain was noted until the 15th.   From the 15th to the 19th of July 0.51 inch of rain was recorded, 0.43 of it falling on the 15th.   Traces of rain were noted at intervals during the rest of the month and the first part of August, but no water of consequence fell until August 9, when 0.54 inch was recorded.   A small amount of rain was again recorded on August 17 and 19, but no appreciable amount was re-corded until September 4.   Thus there were three distinct periods of rainfall in 1916, namely, the middle of July, August 9, and September 4.

Fruit of Earliana began to ripen July 23; of the F_1 cross, July 27; and of Stone, August 16.   About July 29 the fruit of Earliana and the cross had reached its maximum size, and from then on it rapidly declined in size until August 9, when the second heavy rainfall ap-peared.   Immediately after this the size of the fruit increased until about August 26, when it began to decrease until rain appeared on September 4.

Thus on the clay loam soil at University Farm, St. Paul, a rainfall of 0.5 inch exerted a beneficial influence on the size of the tomato fruits for approximately two weeks, and then its influence began to decline.   From the practical standpoint, these results indicate approxi-mately when and how much water should be applied artificially in order to maintain the size of tomato fruits.   Where the soil is less retentive of moisture and the heat more intense, more frequent water-ings would naturally be required.

INHERITANCE OF DECUMBENT HABIT IN PLANTS OF EARLIANA AND JUNE PINK VARIETIES

The dominance in tomatoes of the standard habit of plant growth over the recessive dwarf condition has been known for many years, but no mention has been made of the difference in the habit of stand-ard plants.   Earliana and June Pink varieties, which are apparently identical except in the color of the fruit, have a more decumbent habit of growth than Bonny Best, Chalk Early Jewel, Buck Tresco, Comet, Beauty, Globe, My Maryland, John Baer, and Stone.   The behavior of this decumbent habit has been observed in nine F_1 crosses between Earliana and normal standard varieties, one F_1 cross between Earliana and a dwarf variety, and one F_1 cross between June Pink and a normal standard, and in every case it has shown complete dominance.   For results obtained in 1915-1917, inclusive, see Table IV.

TABLE IV

Cross	♀	♂	F₁ cross
Beauty × Chalk Early Jewel..............	N*	N	N
Chalk Early Jewel × Beauty..............	N	N	N
Beauty × Earliana........................	N	D	D
Beauty × My Maryland...................	N	N	N
Bonny Best × Comet.....................	N	N	N
Bonny Best × Earliana...................	N	D	D
Buck Tresco × Earliana..................	N	D	D
Chalk Early Jewel × Earliana............	N	D	D
Chalk Early Jewel × My Maryland........	N	N	N
Comet × Earliana........................	N	D	D
Dwarf Aristocrat × Stone................	U	N	N
Earliana × Dwarf Aristocrat.............	D	U	D
Earliana × Globe........................	D	N	D
Earliana × My Maryland.................	D	N	D
Globe × Comet..........................	N	N	N
Globe × Dwarf Aristocrat...............	N	U	N
John Baer × Earliana....................	N	D	D
Stone × Earliana........................	N	D	D
Stone × June Pink.......................	N	D	D
Stone × My Maryland....................	N	N	N

* N=Normal standard; D=Decumbent standard; U=Upright or dwarf.

From the practical standpoint the knowledge of the dominance of this decumbent habit has a value, for it furnishes a check to the accuracy of crossing when either the Earliana or June Pink is used in crosses. Further, the decumbent habit may exert an effect on the earliness of ripening, as the fruits on such plants are more exposed to the sun's rays.

COMMERCIAL POSSIBILITIES OF FIRST–GENERATION CROSSES

Whether or not first generation crosses will be used for commercial purposes depends primarily upon whether the returns will compensate for the use of such seed. First generation seed must necessarily be expensive, as crossing naturally entails much labor—the buds must be emasculated in the proper stage, that is, before sufficiently mature to shed pollen; and the pollen must be applied artificially. For commercial purposes it may not be necessary to cover the emasculated flower-clusters with paper sacks to prevent undesirable cross- or self-fertilization, since according to Jones (1916), only a small percentage of crossing takes place in a field of mixed varieties.

Considering the fact that only 1742.4 plants are required to an acre when the plants are set 5 feet apart each way, that one ounce contains from 3000 to 4000 seed, and that one tomato may contain several hundred seed, the cost per plant should be comparatively low. One extra bushel of early fruit should cover all extra expense of such seed for an acre. Growers who cater to early markets and who farm high-priced land; and greenhouse men, who have to make as great a profit as possible from every square foot of space, can well afford to use such seed.

ADVANTAGES OF FIRST–GENERATION CROSSES

The commercial assets of first-generation tomato crosses may be briefly summarized as follows: (1) They are often more productive than either parent, and (2) they are often earlier and smoother, especially when Earliana, a very early variety which bears rough fruit, is crossed with a smooth type as Stone or Chalk Early Jewel.

The seedsman can take advantage of the fact that segregation of characters occurs in the second generation, for the grower must return each season if he wishes to secure the same kind of seed. In other words, the seed grower can hold a trade secret by not publishing the parentage, which would be difficult if not impossible to discover.

DISADVANTAGES OF FIRST–GENERATION CROSSES

The chief disadvantages of F_1 crosses are that their seed must necessarily be expensive and that their fruits are likely to average smaller than standard kinds.

FIRST–GENERATION CROSSES WORTHY OF TRIAL

The tests to date have been somewhat unsatisfactory. For instance, one cross will make a particularly fine showing one season and a poorer one the next, that is, the results have not been as consistent as desired. Whether the variation is partly due to a different reaction toward different climatic changes is unknown, but such an explanation is probable, for it is known that the different varietal strains respond differently to such changes. Without actual trials it is impossible to predict what combinations will give good results. In analyzing the performance of the F_1 crosses grown from 1915 to 1919, it will be found that as a rule crosses between the early varieties, Earliana and June Pink, and the slightly later varieties, Bonny Best, Chalk Early Jewel, and John Baer, have been very productive and in fact have usually produced more fruit than the earlier parent. Since the fruits of these crosses can be classed as smooth, they are more valuable than the

Earliana. As Earliana and June Pink are apparently identical except in color, and Bonny Best, John Baer, and Chalk Early Jewel are of similar type, such crosses are, practically speaking, simply a combination of two types. Since crosses between June Pink and red varieties give red fruits in the first generation, it makes no difference whether this variety or Earliana is used. Another desirable combination, that is, if an early Stone type is wanted, is a cross between Stone and Earliana or June Pink.

Other crosses have done exceptionally well, such as Buck Tresco × Earliana and Comet × Earliana, but as they were tested only one season, it is advisable simply to recommend them for further trial.

For greenhouse purposes, a cross between Bonny Best and Globe proved in one season to be especially valuable. The fruit was smooth and red like Bonny Best, and at least one week earlier. This earliness was probably due partially to the fact that the first blossom cluster set numerous fruits on the cross, and few or none on the parents.

The performance of each cross tested is given in the preceding tables, where its productiveness as well as that of its parents may be learned.

SUMMARY

(1) This bulletin covers a nine-year comparison of first generation crosses with their parents.

(2) The percentage increase of all F_1 crosses, grown each season from 1911 to 1913, over the mean of parents, was respectively 63.62%, 97.43%, and 18.89%.

(3) Sixty F_1 crosses were tested from 1914 to 1919, inclusive, and twenty-one of them ripened a higher percentage of their fruit than their higher parent.

(4) The F_1 crosses on the average ripened more fruits than the mean of their parents and also of their higher parent.

(5) The F_1 crosses on the average produced smaller fruits than the mean of their parents and the higher parent.

(6) The F_1 crosses on the average outyielded the mean of their parents and the higher parent.

(7) The percentage increase for the same cross has fluctuated for the same and different seasons, yet on the average it has given a consistent gain.

(8) Crossing hastened the maturity of the fruits decidedly, that is, when compared with the mean of parents and slightly when compared with the higher parent.

(9) The number of ripe and green fruits produced per plant by mean of parents, higher yielding parent, and F_1 cross is graphically illustrated in Figure 1.

(10) The F_1 fruits derived from crosses between smooth and rough fruited varieties are superior to the fruits produced by the rough fruited parent and are generally classed as smooth.

(11) The yield of tomato varieties and crosses was closely correlated with climatic conditions. The highest yield was obtained in 1913 when the mean temperature of the two growing months, June and July, averaged nearly 70° F. and the rainfall was ample to produce good growth; and the third or ripening month, August, was sufficiently dry and hot to cause a good setting and ripening of fruit.

(12) The high and low yielding strains of Bonny Best, Chalk Early Jewel, Earliana, and Stone, in the cold wet year of 1915, reversed their positions in the hot dry year of 1916.

(13) The number of ripe and green fruits produced from 1915 to 1918 by the mean of parents and F_1 crosses fluctuated directly with the weather conditions of the respective seasons.

(14) In 1916, a hot and dry season, the rainfall came periodically. After a heavy rainfall the size of the fruit increased for approximately two weeks and then decreased in size.

(15) Two types of standard tomato plants, decumbent and normal, were noted, the former behaving as a dominant to the latter.

(16) At least two tomato F_1 crosses could be grown to advantage, namely, (a) a cross between Earliana, or its near relative June Pink, and Bonny Best, John Baer, and Chalk Early Jewel, which are similar in season and appearance; and (b) a cross between the Earliana type and Stone. The former would be very early and smooth and the latter early, smooth, and solid, like Stone.

(17) The increased yield of superior early fruit should more than offset the extra cost of F_1 seed.

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Inheritance and Yield with Particular Reference to Rust Resistance and Panicle Type in Oats

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INHERITANCE AND YIELD WITH PARTICULAR REFERENCE TO RUST RESISTANCE AND PANICLE TYPE IN OATS

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INTRODUCTION

The accumulation of facts concerning inheritance has engaged the attention of a large number of biologists since the rediscovery in 1900 of Mendel's laws. Mendel's laws of inheritance and the genetic facts subsequently discovered are the working tools of the plant breeder. It is true that plants and animals were improved by breeding long before the era of Mendelism, but it was progress without a knowledge of the principles involved. At present the plant or animal breeder has at his disposal a set of facts which suggest the general plan of attacking a particular problem.

Next in order of importance to the fundamental laws of inheritance, is the discovery of the manner of inheritance of a particular character. One can not intelligently outline a project for improving plants or animals with regard to certain characters until something is known of the mode of inheritance of those characters. Extensive contributions have been made in this field as to both morphological and physiological characters.

The breeding of plants for disease resistance will always play an important rôle in the breeding of economic plants. Already much has been accomplished, both as to the discovery of the modes of inheritance of resistance to certain diseases and as to the actual production of disease resistant forms possessing economic value. Of the greatest importance to one who seeks to improve plants by breeding for disease resistance is the fact that this character obeys the same fundamental laws of inheritance as plant characters in general.

The investigation reported in this paper resulted from an attempt to combine resistance to stem rust, *Puccinia graminis avenae,* and high yield in oats. A preliminary survey revealed an oat strain which possessed striking resistance to stem rust but unfortunately had only mediocre yielding ability under conditions which were obtained at University Farm, St. Paul, Minnesota. This resistant strain was crossed reciprocally with two high-yielding susceptible strains. The progenies of these crosses were studied during a period of three years primarily for the purpose of ascertaining the manner of inheritance of resistance to stem rust in oats.

REVIEW OF LITERATURE

Bolley (1901, 1903, 1909), at the North Dakota Experiment Station, pointed out a method of producing flax resistant to wilt, *Fusarium lini*. Seed from disease resistant plants growing on soil known to be infested with the wilt-producing organism was saved and again planted on infested soil. By continuing this practice for a few years, flax resistant to wilt was isolated. Bolley's results have been corroborated at the Minnesota Experiment Station (Stakman, *et al*, 1919).

Tisdale (1916, 1917) has pointed out what an important rôle environment plays in determining susceptibility to flax wilt. High temperatures materially decrease resistance. As the result of a study of the F_1 and F_2 progenies of certain flax crosses the same author suggested that the inheritance of resistance to this disease could be explained by means of multiple factors.

An early attempt to combine disease resistance and high yield was made with the cowpea (Webber and Orton, 1902; Orton, 1902). The variety Iron[1], which is resistant to rootknot, *Heterodera radicicola;* and wilt, *Neocosmospora vasinfecta,* var. *tracheiphila,* was crossed at first with several sprawly unproductive forms and later with upright productive forms. From the later crosses the variety Monetta, which has disease resistance and high-yielding ability, was obtained. Brabham, a variety produced by a farmer, has the same parentage as Monetta, namely, Iron and Whippoorwill, and has consistently shown itself superior to Monetta. Orton (1911) has found that resistance to the above disease is inherited as a dominant character.

Conqueror, an edible variety of watermelon resistant to wilt, *Fusarium niveum,* is the result of a cross between a resistant, non-edible stock melon or "citron" and a susceptible, edible form (Orton, 1911).

In general, resistance to wilt, *Fusarium vasinfectum,* in cotton is inherited as a dominant character (Orton, 1911). Commercial cotton resistant to this disease has been produced by selection for resistance among plants growing on soil infested with the organism causing wilt.

By selecting under disease conditions, Bain and Essary (1906) were able to isolate red clover resistant to anthracnose, *Collectotrichum trifolii.*

Edgerton (1918) and Durst (1918) have been successful in isolating tomatoes resistant to wilt, *Fusarium lycopersici.* Edgerton grew the seedlings under disease conditions and only those showing resistance were transplanted to the field. The field was likewise known to be infested with the fusarium causing the disease. In a cross between two varieties of tomatoes, one resistant, the other susceptible to blossom-end rot, Stuckey (1916) found resistance an inherited character.

[1] Part of the following information was furnished in a letter from Dr. C. V. Piper to Dr. H. K. Hayes.

The F_1 as well as the F_2 generation was not attacked by blossom-end rot. No segregation occurred in the F_2 generation which was made up of 91 individuals coming from five F_1 plants.

Ikeno (1918) has reported that susceptibility to *Leptosphaeria cattanei* in rice is inherited as a dominant character.

At the Wisconsin Experiment Station, cabbage resistant to yellows, *Fusarium conglutinans* Wollenw., has been produced (Jones and Gilman, 1915) (Jones *et al*, 1920). These investigators emphasize the fact that environment influences very markedly the development of the disease. Resistance is relative, not absolute.

Barrus (1918) has made a careful survey of varieties of beans with respect to their relation to anthracnose, *Colletotrichum lindemuthianum*. Two strains of anthracnose were discovered. It was possible to place the varieties of beans into four groups as follows.

(ab) Varieties susceptible to both strain alpha and strain beta.

(aB) Varieties susceptible to strain alpha but resistant to strain beta.

(Ab) Varieties resistant to strain alpha but susceptible to strain beta.

(AB) Varieties showing some resistance to both strains.

Varieties, whose anthracnose reactions are known, have been crossed and the results reported (Burkholder, 1918; McRostie, 1919, 1921). Resistance to either the alpha or beta strain was found to be inherited as a dominant character dependent on a single factor difference for its expression.

McRostie (1921) has also reported the results of an investigation regarding the inheritance of resistance to bean mosaic and dry root rot caused by *Fusarium martii phaseoli* Burk. The F_1 showed a partial dominance of susceptibility to mosaic, and segregation in F_2 indicated a two-factor difference between resistance and susceptibility of the plants used as parents. In the case of dry root rot susceptibility proved dominant and the F_2 generation gave an approximation to a $9:7$ ratio. Nearly all F_2 resistant plants bred true to resistance in F_3.

Resistance to bunt smut, *Tilletia tritici,* in wheat is clearly an inherited character as is shown by the work of Gaines (1918, 1920) at the Washington Experiment Station. In the cross between the varieties Florence and Turkey, forms were obtained in F_2 that showed a higher degree of resistance than the resistant parent. The results indicated that several factor differences were involved in the inheritance of this character.

At the Washington Agricultural Experiment Station (Waskabayashi, 1921) a study was made of the inheritance of resistance to covered smut, *Ustilago laevis avenae*. In a cross between resistant Red Rust-proof oats, *Avena sterilis,* and susceptible Black Tartarian, *Avena*

orientalis, resistance to this disease was inherited as a dominant character. Three F_1 and 112 F_2 plants were grown. No smutted plants were found in the F_1 or F_2 generations and of 107 F_3 families only 12 produced smutted plants.

A rust, *Puccinia asparagi,* at times has been very destructive to asparagus in the eastern United States. Norton (1911-12, 1913) has shown that resistance to the fungus is an inherited character. The variety of asparagus known as Washington (Norton, 1919) is the result of crossed seed produced by highly resistant parents.

Webber, *et al,* (1912) succeeded in isolating strains of timothy resistant to rust, *Puccinia graminis.* The resistant strains were discovered by the plant-to-row method of selection. Eleven of the better sorts were tested at the Minnesota station and were found to be highly resistant to rust altho each strain produced some susceptible plants (Hayes and Stakman, 1919).

Extensive studies of rust resistance in wheat have been carried out. Biffen (1907, 1912, 1917) found susceptibility to stripe rust, *Puccinia glumarum,* dominant over resistance. The F_2 showed monohybrid segregation. In a similar study, Nilsson-Ehle (1911) found the F_1 generation susceptible in some cases, resistant in others, and intermediate in still others. The segregation obtained was explained by means of the multiple factor hypothesis. Three pure line selections of winter wheat have proved resistant to leaf rust under Kansas conditions (Melchers and Parker, 1920). Observations were made over a period of six years.

Results of a study of the inheritance of resistance to stem rust, *Puccinia graminis tritici,* have been reported by Hayes *et al* (1920). Resistant emmers and durums were crossed with Marquis, a susceptible bread wheat. The F_1 of the durum-Marquis cross was as susceptible as the Marquis parent whereas the F_1 of the emmer-Marquis cross was resistant altho not as resistant as the emmer parent. In both cases later generations showed segregation. Evidence of linkage between rust resistance and the durum and emmer spike characters respectively were obtained. In the above study a single rust form was used in making the artificial epidemic.

Waldron (1921), at the North Dakota station, has reported on the inheritance of resistance to stem rust based on a family derived from a cross between durum and common wheats. Segregation occurred and a linkage relation between durum characters and rust resistance was found. In this study no artificial rust epidemic was created.

The existence of a number of biological forms of stem rust differentiated only by their respective reactions to pure lines of wheat has been clearly demonstrated (Stakman *et al,* 1919). The parasitic reaction of each form was found to be constant.

A comparison of oat varieties with respect to their reaction to stem rust, *Puccinia graminis avenae* Erikss. and Henn., and crown rust, *Puccinia lolii avenae* McAlpine, has been made (Parker, 1918). Several varieties of *Avena sterilis* proved resistant to crown rust, while certain strains of *Avena sativa orientalis* proved resistant to stem rust. In crosses of Burt with Sixty Day (Parker, 1920), resistance to crown rust was found to be an inherited character. In F_2, resistant, susceptible, and various intermediate plants were obtained.

A comprehensive survey of oat varieties with respect to their reaction to both stem and crown rusts has been made at the Iowa Agricultural Experiment Station (Durrell and Parker, 1920). Strains of White Russian oats were found to possess a high degree of resistance to stem rust. The average percentage infection of crown rust among the varieties of *Avena sterilis* was less than the average obtained for the varieties of *Avena sativa*. A relation between time of planting and percentage of rust infection was noted. A slightly heavier infection of stem rust was obtained on the later planted oats, whereas the opposite relation was observed with respect to crown rust.

A preliminary note on the present investigation has been published (Garber, 1921).

HISTORY AND METHODS

During the course of a varietal survey of oats with respect to their reaction to stem rust, *Puccinia graminis avenae,* conducted at the Minnesota Agricultural Experiment Station, a strain belonging to the White Russian group of *Avena sativa orientalis* consistently proved to be highly resistant to this rust fungus. Unfortunately, the oat strain possessed only mediocre yielding ability. Because of their high-yielding ability under Minnesota conditions, the varieties Minota and Victory, both *Avena sativa,* were crossed with the rust-resistant White Russian strain.

The pure-line Minota is a selection from an unnamed variety of commercial oats. It matures about the same season as Swedish Select. The branches of the panicle show a tendency to droop when ripe. The seed is white and the straw medium fine. Minota is susceptible to stem rust but has consistently shown itself a high yielder under Minnesota conditions.

Victory, the other high-yielding parent, is a pure-line production of the Svalöf Agricultural Experiment Station, of Sweden. It possesses characteristics common to the Swedish Select group of *Avena sativa*. The panicle is open, rather short, with branches somewhat ascending. The seed is white and the culms medium coarse. Victory, like Minota,

has always shown a high degree of susceptibility to stem rust. In a normal season Victory matures from ten days to two weeks later than early oats such as Kherson and Sixty Day.

The White Russian pure-line strain used as the resistant parent has a side panicle and white seed and is late in maturing. The culms are medium fine and grow somewhat taller than those of Victory or Minota. Altho White Russian has not shown high-yielding ability at University Farm, it has always given evidence of a high degree of resistance to stem rust when this fungus was known to be present.

The susceptible parents and the resistant parent described above were reciprocally crossed in the plant breeding nursery at University Farm, St. Paul, during the summers of 1918 and 1919. Enough F_1 plants were matured in the greenhouse in the winter and early spring of 1918-19 to obtain a small F_2 generation the following summer. This generation and the parents were grown in the plant breeding nursery. They were planted considerably later than the rest of the oat nursery which proved to be a fortunate circumstance. The natural stem rust epidemic which occurred that year attacked particularly the oats later in maturing. When the bulk of the oat nursery had been harvested, the F_2 generation and the parents were still quite green. At intervals of a few days, beginning at heading time, the hybrid and parent plants were sprinkled with water and immediately after sprinkling, small bundles of heavily rusted straw were vigorously rubbed together over the plants. By this means a heavy rust infection was procured on almost all susceptible plants.

The F_3 generation produced by these F_2 plants together with other material used in this study was grown in the plant pathology nursery during the summer of 1920. In 1921, also, the plants studied were grown in the pathology nursery. The artificial rust epidemics created during the summers of 1920 and 1921 were made under the direction of the section of plant pathology.

The rust epidemic was induced by hand inoculation, by spraying, and by distributing throughout the nursery potted oat plants on which the rust fungus had developed previously in the greenhouse. Hand inoculation was practiced only relatively early in the process of bringing about epidemic conditions. By means of a suitable small spatula, uredospores were smeared on the under surface of moistened leaves of the susceptible parents at the region where most rapid leaf growth takes place. As soon as epidemic conditions were apparent, spraying only was practiced. A spray of a suspension of uredospores in water was applied in the evening several times a week until the desired degree of infection was obtained. The suspension was prepared by macerating recently collected, heavily rusted oat stems and leaves in water. Care was taken to apply the spray uniformly on all hybrid plants as well as on the parents.

In 1920, owing to the absence of stem rust on oats early in the growing season, it was necessary to procure uredospores outside of Minnesota. A bundle of oat straw carrying uredospores of *Puccinia graminis avenae* was obtained from Oklahoma. This material, together with some local stem rust which appeared later in the season, was used for the source of the epidemic in 1920. The rusts obtained from the two localities apparently produced the same parasitic reaction with the host plants. Owing to the somewhat adverse season for the development of the fungus and the fact that stem rust was not available early in the season, the epidemic this year was not so severe as desired, altho a moderately uniform infection was obtained.

In 1921 the source of the epidemic was stem rust obtained locally which had been carried through the previous winter on susceptible oat varieties growing in the greenhouse. By means of successive plantings and seedling inoculation it was not difficult to carry the rust in the uredospore stage through the winter. The work of producing an epidemic in the nursery was begun early in the season and proved highly successful. In 1921 an exceptionally severe epidemic of stem rust was obtained.

All the plants grown in connection with this study were planted in five-foot rows and spaced approximately two and one-half inches apart in the rows. The rows were one foot apart. In 1919 the parents were grown on both sides of the small plot containing the F_2 plants. In 1920 each parent grown in two five-foot rows appeared eight times distributed throughout the nursery. In addition to the F_2 and F_3 generations grown this year, 26 F_1 plants were produced and subjected to the rust epidemic. The entire nursery was surrounded with three rows of Victory oats. In 1921 the White Russian parent, again grown in two five-foot rows, appeared six times throughout the nursery. Two rows of each parent were grown at the beginning and at the end of the plot containing the F_2 generation. In the F_3 generation two five-foot rows of the susceptible parent were grown every 12 rows, i. e., Minota with the Minota-White Russian F_3 and Victory with the Victory-White Russian F_3, respectively. In addition a row of Victory was grown on each side of the alley between plot series and at a distance of about six inches from the ends of the five-foot rows. The entire nursery was again surrounded as in the previous year with three rows of Victory. The frequent appearance of the susceptible parents aided in producing a rust epidemic.

In analyzing the data presented in this paper, the method of least squares has been used. All computations involving decimals were carried to the fourth place beyond the decimal and the fourth digit dropped. In calculating the probable errors of Mendelian ratios, two methods were employed. When but two frequency classes were avail-

able, the ordinary formula for computing probable errors was used. If there were more than two frequency classes, the method suggested by Harris (1912) and based on a mathematical criterion evolved by Pearson (1900) was used. The values for "goodness of fit" (P) were taken from Elderton's (1901-02) table.

NATURE OF RESISTANCE TO STEM RUST IN OATS

In a recent issue of Science, Miss Allen (1921) ascribes resistance of Kanred wheat to stem rust, *Puccinia graminis tritici,* obtained from the Berkeley breeding plots, to size of stomatal openings. Measurements of the apertures of stomata on the leaves of Mindum and Kanred seedlings grown in the greenhouse were made. Mindum wheat, which is relatively susceptible to this particular biological form of rust, was found to have stomatal openings of about twice the width of the stomatal openings of Kanred. It is suggested that the cause of resistance in this case is solely morphological, i. e., the stomatal apertures of Kanred are small enough to prevent largely the parasitic fungus from entering the host.

A study somewhat similar to that of Miss Allen was made in the present investigation. Six and seven plants of the Victory and White Russian parents, respectively, together with a single plant of each of three different F_3 families breeding true for rust reaction and panicle type, were examined for size of stomata. The plants were pulled in the nursery about two weeks before harvest and the roots immediately immersed in water. In this condition they were taken to the laboratory and by means of a razor, strips of the epidermis were peeled from the under surface of the green leaves and mounted in distilled water. With a screw micrometer, measurements of the length of the major and minor axes through the guard cells were made. The stomata were measured immediately after the epidermal layer had been removed from the plant. The data for length and breadth of 25 stomata from each plant is presented in Tables I and II respectively.

TABLE I

FREQUENCY DISTRIBUTIONS SHOWING LENGTH OF STOMATA THROUGH THE GUARD CELLS ON THE UNDER SURFACE OF CERTAIN OAT LEAVES

Name	No. of plants	Frequency classes One increment = 0.23μ									Total	Mean	Diff / P. E.*
		155	165	175	185	195	205	215	225	235			
Victory	6	3	32	51	42	16	4	2			150	178.7±0.6	14.0
White Russian	7	1	15	27	32	30	30	16	15	9	175	195.5±1.0	
F_3 open, Re†	1			4	8	5	8				25	191.8±1.5	1.5
F_3 open, Su	1		1	1	6	8	7	2			25	195.0±1.6	
F_3 side, Re	1	2	2	6	5	3	6	1			25	185.8±2.2	0.8
F_3 side, Su	1	1	1	6	4	7	6				25	188.2±1.9	

*In this and subsequent tables, Diff / P. E. is written adjacent to the smaller quantity.
†Re = resistant; Su = susceptible.

The difference between the average lengths of stomata of Victory and White Russian is 14 times its probable error and the difference in breadth of stomata between the means of the same two varieties is 2.8 times its probable error. Apparently White Russian has somewhat longer but slightly narrower stomata than Victory.

The four F_3 plants revealed no significant differences in mean length of stomata between plants of the same panicle type but unlike rust reaction. The F_3, open-panicled, susceptible plant and the F_3, side-panicled, resistant plant showed respectively the longest and the shortest mean lengths of stomata; the difference being 9.2 ± 2.7 or approximately 2.1μ. With the exception of the side-panicled, suscep-tible plant, the F_3 individuals had about the same mean breadth of stomata. A difference 8 times the probable error was found between the means of width of stomata in the two side-panicled plants. The stomata of the resistant plant had a mean width of 13.3μ while that of the susceptible plant was 15.0μ. Owing to the small number of measurements made on the F_3 plants, the means may be considered as approximations only.

TABLE II

FREQUENCY DISTRIBUTIONS SHOWING BREADTH OF STOMATA THROUGH THE GUARD CELLS ON THE UNDER SURFACE OF CERTAIN OAT LEAVES

Name	No. of plants	Frequency classes One increment = 0.23μ											Total	Mean	Diff. P. E.
		47	50	53	56	59	62	65	68	71	74	77			
Victory.......	6		12	21	29	30	33	15	8	2			150	58.8 ± 0.3	
White Russian.	7	1	8	24	60	45	24	8	1	3	1		175	57.7 ± 0.2	2.8
F_3 open, Re...	1			4	8	6	3	3	1				25	58.5 ± 0.6	0.1
F_3 open, Su...	1			4	7	5	7	1	1				25	58.6 ± 0.5	
F_3 side, Re.....	1		4	1	4	9	6	1					25	57.8 ± 0.6	8.0
F_3 side, Su.....	1				1	4	7	4	3	4	1	1	25	65.0 ± 0.7	

In addition to determining the length of the major and minor axes through the guard cells of stomata from plants growing in the nursery, measurements were also made of the width of stomatal openings in seedlings of Victory and White Russian. The seedlings were grown in six-inch pots in the greenhouse and examined about two weeks after planting. By placing the seedlings in a moist chamber under diffused sunlight, the stomata were induced to open fully. In this condition the seedlings were removed and immediately epidermal strips were taken from the under surface of the leaves and fixed in absolute alcohol. Epidermal layers from the leaves of several plants of each of the pure-line parents were examined. The measurement taken was the width of the stomatal opening at the widest point. The results obtained are presented in Table III.

TABLE III

FREQUENCY DISTRIBUTIONS SHOWING WIDTH OF STOMATAL OPENINGS WHEN FULLY OPEN. VICTORY AND WHITE RUSSIAN SEEDLINGS

Name	Frequency classes One increment = 0.23μ											Total	Mean	Diff / P. E.
	17	20	23	26	29	32	35	38	41	44	47			
Victory............	4	21	25	33	11	7						101	24.4 ± 0.3	24.5
White Russian........		1	1	21	26	21	19	11	1	1		102	34.2 ± 0.3	

The stomatal openings of Victory have a mean width of 5.6μ whereas those of White Russian have a mean width of 7.9μ. The latter parent, which is resistant to stem rust, showed wider stomatal openings than the susceptible Victory. The difference is approximately 2.3μ, which is 24.5 times the probable error. If size of stomatal opening prevented the rust mycelium from penetrating the leaf tissue, width of opening would be the limiting factor.

From the data presented above it is apparent that resistance to stem rust in the oat plants examined can not be attributed to relative size of stomatal openings. Moreover the fact that numerous small uredinia develop on the resistant parent as well as the resistant progeny is *prima facie* evidence that the fungus gains admittance to the inner tissues of the host. It seems that the cause of resistance in this case is physiological rather than morphological in nature. This conclusion is in agreement with that of Jakushkina and Vavilov (1912) as a result of a study of size, number, and distribution of stomata in relation to resistance and susceptibility to rust in different varieties of oats.

Stakman (1914) has shown that resistance of wheat to stem rust, *Puccinia graminis tritici,* is due primarily to a physiological relationship between host and fungus.

In oats the surface of the stems, particularly near the nodes of susceptible plants heavily infected, becomes a mass of rust spores. On the other hand similar regions of resistant plants grown under the same conditions show the surface broken with many relatively minute uredinia. The amount of rust found on resistant plants as well as on susceptible plants varied considerably. Many of the resistant plants showed no uredinia whatever. By means of the size of the uredinia formed on the two categories of oat plants, resistant and susceptible, it was possible to make a clear-cut classification on the basis of rust reaction. Rust-infected susceptible plants gave rise to large oblong uredinia (the confluence of many uredinia) producing relatively long lesions in the stem, whereas resistant plants under the same conditions gave rise to minute uredinia varying in size from scarcely visible to the unaided eye to the size of an ordinary pin head. Figure 1 illustrates the difference between resistance and susceptibility to stem rust as the terms are used in the present paper.
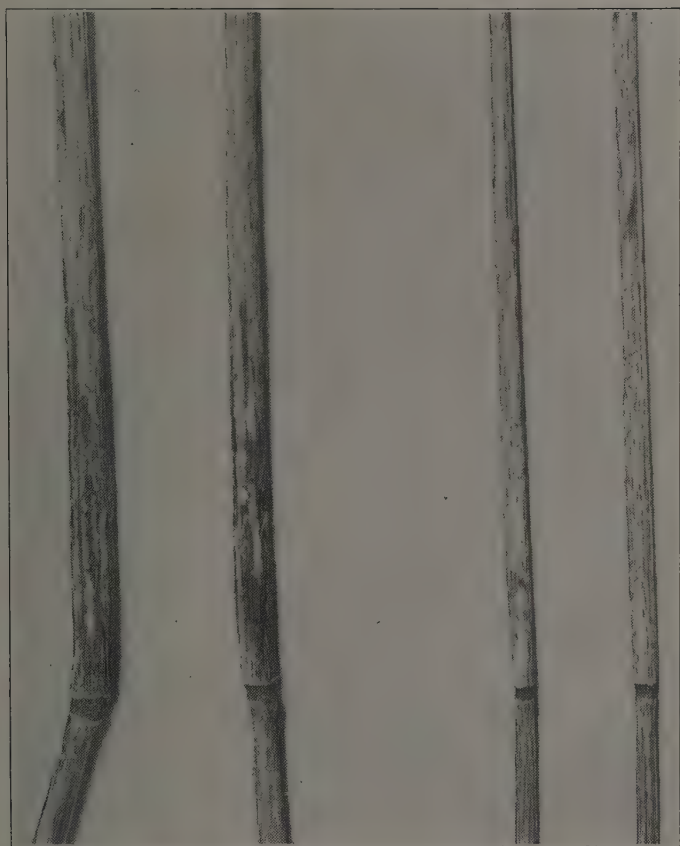
Fig. 1. Types of Reaction to Stem Rust in Oats. At left, two culms of Victory, one of the susceptible parents; two culms of White Russian, the resistant parent. Note the difference in the character and number of uredinia. (Photo by George.)

INHERITANCE OF RUST REACTION AND PANICLE TYPE

The notes on rust reaction and panicle type of all the plants studied except the F_3 generation grown in 1920, were taken in the field immediately after the plants were pulled. The breeding nature of the F_3 generation grown in 1920 was determined while the plants were still standing and just before harvest. Little difficulty was experienced in classifying plants with respect to their rust reaction, but in regard to panicle type the phenotypes were not so clearly differentiated. In the F_3 generations, the families homozygous for open panicles (similar to the parents) were easily determined as they stood out in marked contrast to the other F_3 families.

The reliability of the F_2 classification with respect to the two characters, susceptibility to stem rust and the side panicle type, for all the cultures carried through the F_3 generation, is shown in Tables IV and V, respectively. The number of F_2 plants recorded as side-panicled and the nature of their progeny in F_3 are given. Similar data for rust susceptibility are presented.

In the Victory-White Russian[2] cross, out of a total of 38 F_2 plants classified as susceptible, 35 proved homozygous susceptible, 2 segregated, and 1 bred true for resistance in F_3. The total number of F_3 families homozygous for susceptibility was 37. Of 58 F_2 plants recorded as susceptible in the Minota-White Russian cross, 51 bred true to susceptibility, 5 segregated and 2 were resistant in F_3.

TABLE IV

RELIABILITY OF CLASSIFICATION OF F_2 PLANTS FOR SUSCEPTIBILITY TO RUST ON THE BASIS OF F_3 BREEDING NATURE

| Name | No. of F_2 plants classed as susceptible | F_3 families | | |
		Breeding true for susceptibility	Segregating for rust	Breeding true for resistance
Victory-White Russian..............	38	35	2	1
Minota-White Russian...............	58	51	5	2

A total of 59 F_3 families proved homozygous for susceptibility. Altho there were several F_2 plants wrongly classified in both crosses, the total number of F_2 plants noted as susceptible in F_2 and the total number of F_3 families which proved homozygous for susceptibility closely correspond. Considering both crosses these totals are the same, 96 susceptible F_2 plants and 96 F_3 families homozygous for susceptibility.

With respect to panicle type, greater discrepancies occurred between the F_2 classification and the actual genotypic condition as revealed by the F_3 progeny. In the Victory-White Russian cross 26 F_2 plants were

[2] Where the symbol "—" is used, word order has no significance as to parentage, i. e., male or female. Such a compound word may indicate a particular cross, the reciprocal, or both.

noted as having side panicles but only 17 proved homozygous and 9 segregated in F_3. In all, 27 F_2 plants bred true in F_3 for the side panicle character. In the Minota-White Russian cross, of 29 F_2 plants recorded as having side panicles, 24 bred true and 5 segregated in F_3. However, the F_3 generation of this cross revealed 39 families homozygous for the side-panicled type. The total number of F_2 plants in both crosses noted as side-panicled forms was 55, whereas the number of F_3 families breeding true for side panicles was 66.

TABLE V

RELIABILITY OF CLASSIFICATION OF F_2 PLANTS FOR PANICLE TYPE ON THE BASIS OF F_3 BREEDING NATURE

Name	No. of F_2 plants classed as side panicle	F_3 families	
		Breeding true for side panicle	Segregating for panicle character
Victory-White Russian............................	26	17	9
Minota-White Russian.............................	29	24	5

THE PARENTS AND THE F_1 GENERATION

During the three years that this investigation was in progress the approximate numbers of parental plants grown and studied with respect to their rust reaction and panicle type were as follows: 500 White Russian, 1000 Victory and 1000 Minota. The Victory and Minota plants without a single exception had open panicles (see Fig. 2) and showed large oblong uredinia of stem rust. On the other hand a careful examination of the 500 side-panicled plants of White Russian revealed none, few, or many minute uredinia.

All the F_1 plants except 26, were grown in the greenhouse and were not infected with stem rust. In 1920, 26 F_1 plants made up as follows: 2 White Russian $\times$ Victory[3], 5 Minota $\times$ White Russian, and 19 White Russian $\times$ Minota, were grown in the rust nursery and subjected to the same stem rust epidemic as the F_2, F_3, and parental plants. These F_1 plants showed the rust reaction characteristic of the White Russian parent, namely, a high degree of resistance. A few small uredinia were found on some of the F_1 plants. The evidence obtained from the F_1 generation shows that resistance to stem rust in the above crosses is inherited as a dominant character. With respect to panicle type, the F_1 plants were open, altho not so open as the open-panicled parents.

[3] The female parent is written first where the symbol x is used.
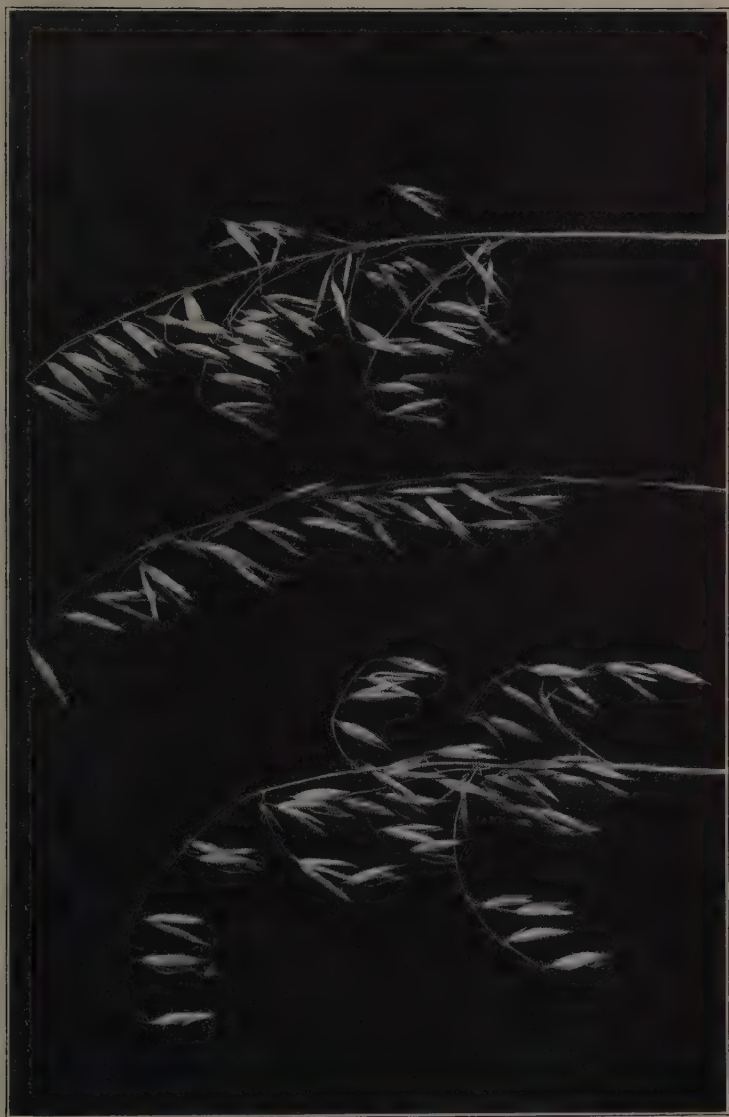
Fig. 2. Panicle Types of the Oats Used as Parents. Left to right,
Minota, White Russian and Victory

THE F_2 GENERATIONS GROWN IN 1920 AND 1921

In Table VI is given a record of all F_2 plants grown in 1920 except those which were propagated in F_3. The data on each F_2 family were kept separate and later combined, as all the families showed they were crosses and gave similar results. The segregation with respect to rust reaction in the White Russian $\times$ Victory and reciprocal crosses is clearly that of a monohybrid showing complete dominance. Among the open-panicled plants there were 452 resistant and 141 susceptible, while among the side-panicled plants there were 115 resistant and 35 susceptible; the quotients of the deviations from the theoretical ratios divided by the probable errors being 1.0 and 0.7 respectively. In other words, deviations as great as these would be expected in about half the cases. In the Minota $\times$ White Russian cross, theory and observation do not agree so well. Among the open-panicled plants there were 466 resistant and 115 susceptible individuals, and among the side-panicled plants 69 resistant and 15 susceptible. The deviation with respect to segregation for rust in the open-panicled types is 4.3 times the probable error and in the side-panicled types 2.2 times the probable error. The Minota-White Russian cross matured on the average about a week earlier than the Victory-White Russian cross. It is probable that some of the F_2 plants of the former cross escaped infection in 1920 owing to the lateness of procuring rust epidemic conditions in the nursery.

TABLE VI

SEGREGATION WITH RESPECT TO RUST REACTION AND PANICLE TYPE IN THE F_2 GENERATION OF
CERTAIN OAT CROSSES GROWN IN 1920

Name	Panicle type	Resistant plants	Susceptible plants	Total
White Russian x Victory	open	255	76	331
White Russian x Victory	side	70	21	91
Victory x White Russian	open	197	65	262
Victory x White Russian	side	45	14	59
Minota x White Russian	open	466	115	581
Minota x White Russian	side	69	15	84

The inheritance of panicle type can not be ascertained from the F_2 generation. Altho all plants were classified with respect to their panicles as open or side, it was evident that many plants showed more nearly an intermediate condition. In this investigation the F_2 intermediate panicle types were classified as open. In the crosses, White Russian $\times$ Victory and reciprocal, there were 593 and 150 F_2 plants classified as open and side, respectively, whereas in the Minota $\times$ White Russian cross 581 plants were classed as open and 84 as side. In the first case the deviation from a monohybrid ratio is 4.5 times the probable error and in the second 10.9 times the probable error. Assuming a single factor difference for panicle type in the

parents, the divergencies of the actual from the theoretical ratios in the F_2 of both crosses is too great to be attributed to the errors of random sampling. Fewer side-panicled plants were classified as such than would be expected on the basis of monohybrid segregation.

Nilsson-Ehle (1908) attributed the difference between open-panicled and side-panicled varieties of oats to two main factors. In the absence of both factors forms with side panicles are produced, whereas if one or both factors are present, forms with open panicles result.

In 1921 a severe epidemic of stem rust was obtained in the nursery. The data on all the F_2 plants grown that year, except those which were propagated in F_3, are shown in Table VII. In general, the segregation with respect to rust reaction corroborates that observed in 1920. The only group of plants showing a considerable deviation from expectation is the side-panicled types of the White Russian-Victory cross. In this group there were 53 resistant and 32 susceptible plants. Here the deviation is 4 times the probable error but only a relatively small number of plants is involved. It is interesting to note that altho the resistant parent has a side panicle, the number of susceptible plants with side panicles in the F_2 of the White Russian-Victory cross is in excess of expectation on a monohybrid basis. In F_2 the ratio of resistant to susceptible plants in the open-panicled group of the White Russian-Victory cross is 327:103, in the open-panicled group of the Minota-White Russian cross 505:147, and in the side-panicled group of the Minota-White Russian cross 72:20. The deviations from the theoretical ratios are respectively 0.7, 2.1, and 1.1 times the probable errors. Divergencies as great as these may reasonably be expected owing to the errors of random sampling.

TABLE VII

Segregation with Respect to Rust Reaction and Panicle Type in the F_2 Generation of Certain Oat Crosses Grown in 1921

Name	Panicle type	Resistant plants	Susceptible plants	Total
White Russian x Victory	open	327	103	430
White Russian x Victory	side	53	32	85
Minota x White Russian	open	232	64	296
Minota x White Russian	side	48	11	59
White Russian x Minota	open	273	83	356
White Russian x Minota	side	24	9	33

The data with regard to segregation for panicle type in F_2 (Table VII) are similar to those obtained the previous year (Table VI). There is a smaller number of plants with side panicles than would be expected on the basis of monohybrid segregation. In the cross, White Russian $\times$ Victory, 430 F_2 plants were classed as open and 85 as side, whereas in the F_2 generation of the crosses, Minota $\times$ White Russian and reciprocal, 652 plants were classed as open and 92 as side. The deviations of these two ratios from a 3:1 ratio are 6.6 and 11.8,

respectively, times their probable errors. The deviations of actual from calculated ratios are significant and can not be explained on the basis of chance.

THE F_3 GENERATIONS GROWN IN 1920 AND 1921

The genotypes with regard to rust reaction and panicle type of all the F_2 plants grown in 1919 and of 200 F_2 plants grown in 1920 were determined in 1920 and 1921, respectively, by the F_3 breeding test. A few F_3 families, grown in 1920, were discarded because they contained too few plants.

In the appendix Tables XXIII to XXV, inclusive, is contained the record of the F_3 Victory-White Russian cross and in Tables XXVI to XXIX, inclusive, the record of the F_3 Minota-White Russian cross. The number of plants and their rust reaction are shown for each F_3 family. With respect to panicle type, the F_3 families are classified as homozygous open, homozygous side, or segregating. An examination of the tables shows that F_3 families homozygous for both open panicle and resistance to rust, F_3 families homozygous for both side panicle and susceptibility to rust, and homozygous F_3 families similar to the parental forms in rust reaction and panicle type were easily obtained.

A summary of the analysis of inheritance of rust reaction and panicle type based on the segregation in F_2 as revealed by the F_3 breeding test, is presented in Table VIII (see appendix Table XXX). The F_2 plants are grouped on the basis of rust reaction into three classes, homozygous resistant, heterozygous resistant, and homozygous susceptible. Each of these groups is further classified on the basis of panicle type into three categories, open panicles, segregating, i. e., producing, both open and side panicles in F_3, and side panicles.

The Victory-White Russian cross produced 38 homozygous resistant, 65 heterozygous resistant, and 37 homozygous susceptible plants in the F_2 generation. Homozygous and heterozygous resistant plants have the same phenotype and can be distinguished only by their respective progenies. The above ratio is in close agreement with that expected on the basis of a single factor difference between resistance and susceptibility. The value of X^2 ($X^2 = 0.728$) is less than one, hence, the probability (P) is relatively great that the deviation is owing to errors of random sampling. In the Minota-White Russian cross 68 homozygous resistant, 110 heterozygous resistant, and 59 homozygous susceptible F_2 plants were produced. Closeness of fit (P) to the theoretical 1:2:1 ratio is 0.3910. In other words, a divergency as great as this would be expected in about two cases out of five solely from the errors of random sampling. Of the 377 F_2 plants from both crosses tested in F_3, about one fourth bred true to resistant, one half again segregated in the ratio of three resistant plants to one

susceptible plant, and one fourth bred true to susceptibility. (See Fig. 3.)

In the Victory-White Russian cross, the F_3 families showed that segregation of panicle types in F_2 was approximately in accordance with monohybrid expectation. Of 140 F_3 families, 33 and 27 were

TABLE VIII

SUMMARY SHOWING SEGREGATION OF F_2 PLANTS WITH RESPECT TO RUST REACTION AND PANICLE TYPE AS REVEALED BY THEIR F_3 PROGENIES

Name	Panicle type	Rust reaction			Total
		No. of F_3 families			
		Re.*	Seg.	Su.	
Victory-White Russian.............	Homo open	7	14	12	33
Victory-White Russian.............	Segregating	24	40	16	80
Victory-White Russian.............	Homo side	7	11	9	27
Total........................	....	38	65	37	....
Minota-White Russian.............	Homo open	23	26	16	65
Minota-White Russian.............	Segregating	35	65	33	133
Minota-White Russian.............	Homo side	10	19	10	39
Total........................	....	68	110	59	....

*Re = resistant; Seg = segregating; Su = susceptible.

homozygous open and side, respectively, while the remaining 80 families again segregated for panicle type. The probability ($P= 0.1905$ is about one in five that the deviation of this ratio from the theoretical $1:2:1$ is owing to chance. In the Minota-White Russian cross, theory and observation do not agree. There is only about one chance in 100 that a deviation ($P= 0.0100$) as great as was obtained is because of random sampling. Sixty-five F_3 families were homozygous open, 133 segregated for panicle type, and 39 were homozygous side. If the segregating families are grouped with the side-panicled families, the ratio becomes 65 open to 172 non-open F_3 progenies. In this case the deviation from a $1:3$ ratio divided by the probable error is 1.3; hence, the deviation is of little significance. The inheritance of panicle type in both these crosses seems to be controlled by one main factor difference. More evidence is needed to determine whether or not there are supplementary factors involved (see Figs. 4 and 5).

A summary of all the data on rust reaction in the F_3 families segregating for this character is shown in Table IX. The relative numbers of resistant and susceptible plants in each family were determined. An examination of the column containing the quotients of the deviations divided by their respective probable errors shows that theory and observation, with two exceptions, agree very well. In cultures 2-2-1, etc., the deviation is 5.8 times the probable error and therefore significant. If families 2-2-1, 2-2-14, and 2-2-42, which produced more susceptible than resistant plants are eliminated from cultures 2-2-1, etc., the ratio of resistant to susceptible plants becomes 662 to 227 respectively. In this instance Dev./P.E. is $4.75/8.708 = 0.5$.

Fig. 3. Oat Culms of Victory, White Russian, and Two F₃ Families of a Cross Between Them Homozygous for Rust Reaction Left to right, White Russian, susceptible F₃, resistant F₃, and Victory

TABLE IX

SUMMARY SHOWING SEGREGATION WITH RESPECT TO RUST REACTION IN ALL THE SEGREGATING F_3 FAMILIES

Name	Culture number	Year grown	No. of plants		No. of plants expected (3:1)		Dev./ P. E.
			Resistant	Susceptible	Resistant	Susceptible	
White Russian x Victory..	2-13-1, etc.	1920	500	177	507.75	169.25	1.0
White Russian x Victory..	2-2-1, etc.	1921	691	301	744.00	248.00	5.8
Victory x White Russian..	3-1-1, etc.	1921	567	203	577.50	192.50	1.3
Total..............	....	......	1758	681	1829.25	609.75	4.9
Minota x White Russian...	4-7-1, etc.	1920	953	237	892.50	297.50	6.0
Minota x White Russian...	4-8-1, etc.	1920	1026	357	1037.25	345.75	1.0
Minota x White Russian...	4-9-1, etc.	1920	823	259	811.50	270.50	1.2
Minota x White Russian...	4-4-1, etc.	1921	1404	436	1380.00	460.00	1.9
Total..............	....	......	4206	1289	4121.25	1373.75	3.9
Total for both crosses.....	....	......	5964	1970	5950.50	1983.50	0.5

In cultures 4-7-1, etc., the divergence from expectation is six times the probable error. It is likely that a number of plants in these families were recorded as resistant because of their escape from rust infection. The rust epidemic in 1920, as has been pointed out, was somewhat light. Considering the total of all the plants in both crosses grown in 1920 and 1921, there were 5964 resistant and 1970 susceptible F_3 plants in the cultures segregating for rust reaction. In this case Dev./P.E. is 0.5. Resistance to stem rust in the above crosses is inherited as a dominant character showing monohybrid segregation among the progeny from individuals heterozygous for rust reaction.

RELATION BETWEEN PANICLE TYPE AND RUST REACTION

If the factor difference for rust reaction and panicle type in the above crosses were closely linked in inheritance, it would be necessary to produce a comparatively large number of F_2 plants to obtain open-panicled, rust-resistant individuals. Such was not the case, as an examination of Table VIII shows. Of 38 homozygous resistant F_2 plants in the Victory-White Russian cross, 7 bred true to open panicles and 7 to side panicles in the next generation. The 37 homozygous susceptible F_2 plants produced 12 and 9 F_3 families homozygous for open and side panicles respectively, and 16 F_3 families which segregated for panicle type. In the Minota-White Russian cross, the homozygous resistant F_2 plants gave 23, 35, and 10 homozygous open, segregating, and homozygous side F_3 families respectively. In the same cross the homozygous susceptible F_2 plants produced 16, 33, and 10 F_3 families breeding true for open panicles, segregating for panicle type and breeding true for side panicles respectively (see Figs. 4 and 5).

In the discussion of Tables VI and VII it was pointed out that the F_2 plants classified as side-panicled forms with one exception showed monohybrid segregation with respect to rust reaction. The one excep-

tion, White Russian $\times$ Victory F_2 grown in 1921, produced more side-panicled, susceptible plants than would be expected on the basis of independent segregation. The same general relation was observed between open-panicled F_2 plants and their reaction to rust altho here again one exception appeared. More open-panicled, Minota $\times$ White Russian F_2 plants grown in 1920, were recorded as resistant to rust than were expected on the basis that rust reaction and panicle type were independently inherited. In both exceptions, however, the combination of the particular rust reaction and panicle type is opposite to the combination of these characters found in the parents, namely, side panicles with resistance and open panicles with susceptibility.

Part of the data collected in connection with a study of the relation of yield to rust reaction and to panicle type in the F_3 families grown in 1921 is of interest here. The plants in each F_3 family segregating for both rust reaction and panicle type were classified as open-panicled resistant, open-panicled susceptible, side-panicled resistant, and side-panicled susceptible. The data for the Minota-White Russian cross are presented in Table X. On the assumption that rust reaction and panicle type are independently inherited, one would expect a 9:3:3:1 ratio. The ratio for the total number of plants was 516 open-panicled resistant : 162 open-panicled susceptible : 166 side-panicled resistant : 61 side-panicled susceptible. The goodness of fit in this experiment is very close, the value of X_2 being less than one $(X_2 = 0.871)$.

TABLE X

SEGREGATION WITH RESPECT TO RUST REACTION AND PANICLE TYPE IN CERTAIN F_3 FAMILIES OF MINOTA X WHITE RUSSIAN, GROWN IN 1921

Culture number	No. of Plants			
	Open Panicle		Side Panicle	
	Re	Su	Re	Su
4–4– 7	16	6	9	4
4–4–10	20	7	8	4
4–4–13	15	10	9	2
4–4–14	15	9	9	4
4–4–15	26	10	7	2
4–4–22	17	7	9	3
4–4–29	23	9	8	3
4–4–30	23	9	5	1
4–4–34	24	7	9	3
4–4–36	23	8	6	1
4–4–39	26	5	11	1
4–4–41	28	5	9	1
4–4–48	23	3	4	4
4–4–57	22	12	6	4
4–4–68	17	4	6	3
4–4–70	23	9	6	3
4–4–71	29	4	6	2
4–4–74	20	6	10	2
4–4–77	26	8	5	2
4–4–88	26	5	9	3
4–4–91	18	6	5	5
4–4–96	30	6	2	3
4–4–97	26	7	8	1
Total......	516	162	166	61
Expectation (9:3:3:1)	509.063	169.688	169.688	56.563

$x^2 = 0.871.$ $P = $ close fit.

Fig. 4. Representative Panicles Obtained in Two F₃ Families Homozygous for Rust Resistance
and Panicle Type in the Cross White Russian x Victory
Left to right, open panicle and side panicle
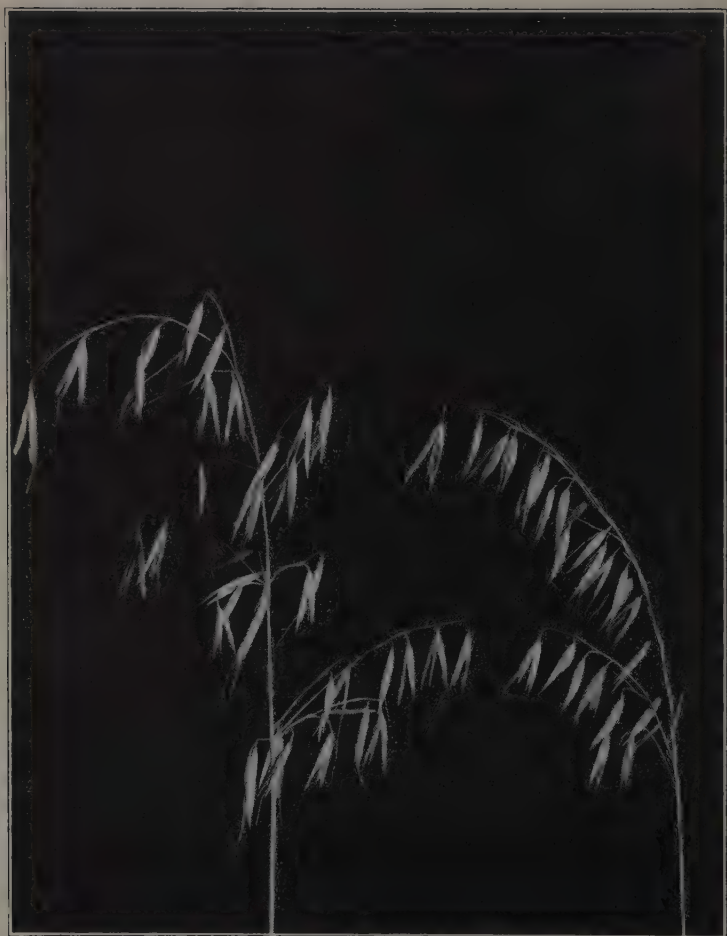
Fig. 5. Representative Panicles Obtained in Two F_3 Families Homozygous for Panicle Type in the Cross Minota x White Russian. Left to right, open panicle of susceptible family and side panicle of family segregating for rust.

Similar data for the White Russian-Victory cross are shown in Table XI. It will be noted that four F_3 families segregating for both rust reaction and panicle have been eliminated from this table. These families were arbitrarily omitted because they showed more susceptible than resistant plants. The total number of plants were classified as follows: 657, 187, 156, and 82 open-resistant, open-susceptible, side-resistant, and side-susceptible respectively. In this case the deviation from the theoretical 9:3:3:1 is so great that the probability of this divergency being due solely to the errors of random sampling is very remote. On the basis of chance such a deviation ($P = 0.0003$) would be expected to occur in only about three out of 10,000 cases. Considering the open-panicled group and the side-panicled group separately, it is of interest to note that on the basis of independent segregation the resistant plants are in excess in the former and the susceptible plants in the latter group. Again the combination of rust reaction and panicle type are opposite to that found in the parents. In an F_3 generation such a relation might arise because of cross-overs between linked

TABLE XI
SEGREGATION WITH RESPECT TO RUST REACTION AND PANICLE TYPE IN CERTAIN F_3 FAMILIES
OF WHITE RUSSIAN x VICTORY AND THE RECIPROCAL, GROWN IN 1921

Culture number*	No. of plants			
	Open panicle		Side panicle	
	Re	Su	Re	Su
2–2–2	22	4	5	1
2–2–3	26	6	4	3
2–2–5	25	7	6	3
2–2–11	25	5	8	2
2–2–19	22	9	2	4
2–2–21	22	7	5	4
2–2–22	23	7	5	4
2–2–23	27	6	4	2
2–2–31	20	11	2	4
2–2–36	20	6	6	3
2–2–38	19	6	10	2
2–2–39	21	5	3	4
2–2–41	18	5	5	2
2–2–44	15	9	2	2
2–2–46	19	6	10	0
2–2–47	21	5	4	1
2–2–49	17	6	9	4
3–1–11	19	5	9	3
3–1–13	23	7	5	5
3–1–14	25	6	4	2
3–1–18	16	3	5	3
3–1–22	27	5	6	2
3–1–27	19	5	2	2
3–1–28	16	10	3	4
3–1–31	22	6	4	3
3–1–38	30	3	4	3
3–1–40	21	8	3	3
3–1–41	19	6	6	1
3–1–43	22	7	5	1
3–1–44	24	4	6	2
3–1–48	12	2	4	3
Total......	657	187	156	82
Expectation (9:3:3:1)	608.625	202.875	202.875	67.625

$P = 0.0003$
*Families 2–2–1, 2–2–14, 2–2–42, and 3–1–3 omitted.

factors in the F_1 plants. Such an explanation for the above instance is untenable, particularly when all the evidence is considered. It i more probable that some of the F_2 plants classed as side-susceptible should have been classed with the open-susceptible group. Then, too the number of plants classed as side-panicled is relatively small.

In view of the data presented, the two characters, rust reaction and panicle type, are not closely linked in inheritance. The factor difference controlling reaction to stem rust and the main factor difference controlling panicle type are either located in different chromosome pairs or, if in the same chromosome pair, the factors cross over frequently

INHERITANCE OF POLLEN ABORTION

The Victory, Minota, and White Russian parents, together with representatives of the F_1, F_2, and F_3 generations grown in the nursery in 1920, were examined for aborted pollen. Florets in which the anthers were about ready to dehisce, were collected in the field and taken to the laboratory. Here the anthers were placed on slides and allowed to dehisce. This usually occurred a few moments after their removal from the florets. When the anthers proved too immature, a new sample was obtained. The pollen was mounted in an aqueous solution of acid fuchsin and lactic acid. Aborted pollen is not stained with this solution.

The percentage of aborted pollen on each slide was determined by making from five to fifteen counts of random samples each consisting of 100 pollen grains. The larger number of counts was made on the slides showing the greater percentages of aborted pollen. Each slide except those of the F_3 individuals contained pollen from a single plant. A preliminary examination revealed comparatively little variability of percentage aborted pollen in different anthers from the same plant. In view of this, but one or two anthers were used to constitute the pollen sample of a single plant.

Frequency distributions of the percentage aborted pollen in parental, F_1, and F_2 plants are shown in Table XII. The 10 plants of each White Russian and Minota showed an average of about one per cent sterile pollen whereas the 29 Victory plants showed an average of 12.4 per cent. In the 11 White Russian-Minota F_1 plants less aborted pollen was found than in the parents. A similar condition was observed in 42 F_2 plants of the same cross. In the White Russian-Victory cross only one F_1 plant was examined and it revealed 3.5 per cent aborted pollen. The range of the percentage of unstained pollen grains in the F_2 generation of this cross was from less than one to 14.5 per cent whereas the range in the Victory parent was from 8.5 to 18.5 per cent.

TABLE XII

Frequency Distributions of Percentage Aborted Pollen in Parents and Progenies of Certain Oat Crosses. Each Determination Made from a Single Plant

Name	Culture number	Frequency classes. Percentages of aborted pollen																			Total number of plants	Mean	S. D.	C. V.
		0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5	15.5	16.5	17.5	18.5				
White Russian, P₁		6	4																		10	0.9		
Minota, P₁		7	2		1																10	1.0		
Victory, P₁										1	4	7	5	3	1		5	1	1	1	29	12.4±0.3	2.7±0.2	21.8±1.9
White Russian x Minota, F₁		10																			10	0.5		
Minota x White Russian, F₁		1																			1	0.5		
White Russian x Victory, F₁					1																1	3.5		
Minota x White Russian, F₂	2-2-1 to 2-2-125	39	3																		42	0.6		
White Russian x Victory, F₂	3-1-1 to 3-1-125	8	40	24	20	12	11	4	2	1	3	1			1	1					125	3.2±0.1	2.3±0.1	71.9±3.1
Victory x White Russian, F₂		17	41	27	18	8	9	2	2			1									125	2.6±0.1	1.8±0.1	69.2±3.0

Of the 250 F_2 plants examined, only 7 showed percentage of aborted pollen within the range shown by the Victory parent. The mean percentage of sterile pollen in the Victory parent is approximately four times the mean of the F_2 generation. The absolute variability as measured by the standard deviations does not show a very great difference between the two groups of plants but the relative variability shows considerable difference. The F_2 generation has a coefficient of variability about three times that of the Victory parent. The segregation observed in the F_2 generation indicated that aborted pollen as found in the Victory parent was inherited as a recessive character involving at least two factors. More evidence is needed to establish with certainty the mode of inheritance of this character.

In order to determine if high percentages of aborted pollen were closely associated with panicle type, 7 F_3 families homozygous for open panicles and 7 F_3 families homozygous for side panicles were examined. An average of 20 counts of 100 pollen grains each was made on composite samples of pollen taken from different plants of the same culture (F_3 family). The number of plants from which the composite sample of pollen was collected, the panicle type, and the average percentage of aborted pollen for each F_3 family are shown in Table XIII. The open-panicled F_3 families exhibit a wider range of percentage sterile pollen than the side-panicled F_3 families, but the means of the average percentages are approximately the same for the open- and side-panicled forms. The mean for the open type is 3.7 and for the side type 3.8 per cent aborted pollen. In this connection it is of interest to point out that of the seven F_2 plants showing percentages of aborted pollen within the range exhibited by the Victory parents, six were classed as open-panicled and one as side-panicled. No evidence of a close association in inheritance between panicle type and pollen abortion was found. (See Fig. 6.)

TABLE XIII

AVERAGE PERCENTAGE OF ABORTED POLLEN IN DIFFERENT F_3 FAMILIES HOMOZYGOUS FOR PANICLE TYPE IN THE CROSS WHITE RUSSIAN X VICTORY. EACH DETERMINATION MADE FROM APPROXIMATELY 20 COUNTS OF 100 POLLEN GRAINS EACH

Culture number	No. of plants	Average percentage of aborted pollen	
		Panicle type	
		Open	Side
2-13- 2	15	. . .	3.7
2-13- 7	15	1.6	. . .
2-13-12	15	. . .	5.1
2-13-16	15	. . .	2.5
2-13-19	15	3.0	. . .
2-13-20	15	. . .	3.4
2-13-26	13	. . .	4.7
2-13-27	6	7.4	. . .
2-13-31	15	. . .	5.5
2-13-32	15	0.7	. . .
2-13-33	6	1.3	. . .
2-13-34	6	6.1	. . .
2-13-37	15	5.6	. . .
2-13-39	15	. . .	2.0
Average	. . .	3.7	3.8
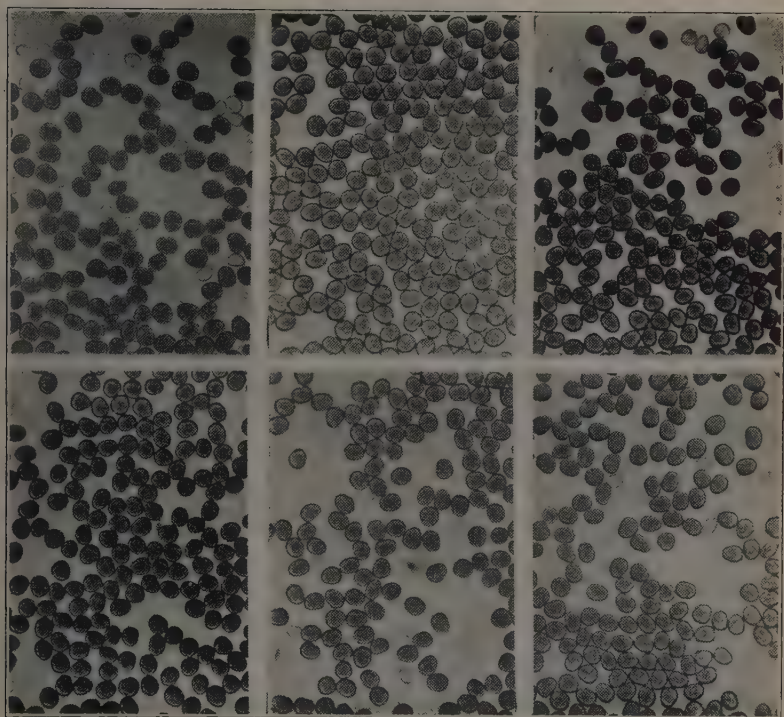
Fig 6. Photomicrographs Showing Aborted Pollen in Oats. From left to right, upper row, Victory parent, White Russian parent, and F_8 cross between them; lower row, three different F_2 plants of the same cross. Aborted pollen appears clear in the plate.

YIELD IN RELATION TO RUST AND PANICLE TYPE

It is commonly conceded that stem rust decreases yield. Estimates have been made from time to time of the damage caused by this fungus but little experimental data have been collected. Bluestem wheat, at the North Dakota Experiment Station (Walster, 1921) gave an annual average yield of 7.1 bushels per acre during five rust years and 26.7 bushels per acre during five non-rust years. During the ten-year period from 1911 to 1920, inclusive, stem rust of wheat was epidemic in Minnesota in 1916, 1919 and 1920[4]. The average yield for these years was 8.6 bushels while for the seven remaining years the average yield was 15.4 bushels.

In the variety tests conducted at University Farm, the open-panicled oats have generally yielded more than the side-panicled forms. The varieties Victory and Minota, which have open panicles, have consistently showed yielding ability superior to that of the White Russian variety, a side-panicled form.

The material grown in 1921 in connection with the study of the inheritance of rust reaction and panicle type, was particularly suitable for studying the relation of these characters to yield. The parents and all the F_3 families except one were grown in plots consisting of two five-foot rows. Because of the small quantity of seed, one F_3 family was grown in a single five-foot row. The planting plan of that part of the nursery which contained the F_3 families is shown in Tables XXXV and XXXVI in the appendix. Some of the F_3 families were eliminate from the yield study, because of the relatively large number of injured plants. In the other F_3 families, the F_2 generation, and the parents, no plant which showed the loss of a panicle was harvested for yield.

The plants at the end of each row did not show noticeable border effect, owing undoubtedly to the fact that a drilled row of Victory was grown on each side of the alleys between plot series. The drilled rows of Victory were grown at a distance of about six inches from the ends of the plots. Moreover, the number of plants involved in this study is such that influence of border would not materially change the relative difference between average yields of the different classes of plants, i. e., between open resistant and open susceptible, etc. In view of these considerations, plants growing at the ends of the plots were not omitted from the yield study.

All the F_2 generations and all but three of the F_3 families homozygous for rust resistance were harvested as individual plants and their yields determined.

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[4] From summaries on yields furnished by the courtesy of Professor Andrew Boss.

The other F_3 families and the parents were harvested and bulk yields of each plot ascertained. The plants of each plot showing segregation for either panicle type or rust reaction or for both characters were classified as open resistant, open susceptible, side resistant, and side susceptible. After noting the number of plants, the panicles of each class of plants were removed and placed in separate muslin bags. The parents and the F_3 families homozygous for rust reaction and panicle type, except those of which individual plant yields were determined, were harvested in a similar way. In this case there was of course but one class of plants in each plot. When dry both the individual plants and the bulk samples were threshed in an individual plant thresher.

INDIVIDUAL PLANT YIELDS

The relation of rust reaction and panicle type to yield in the F_2 generation is shown in Tables XIV and XV. The frequency distribution, number of plants, and mean yields are shown for each class of plants in each of the two different crosses. The significance of the differences between mean yields based on rust reaction may be ascertained from the column at the extreme right of each table. The quotient of the difference divided by its probable error appears adjacent to the smaller quantity.

In the open-panicled forms (Table XIV) of the Victory-White Russian cross the resistant plants yielded an average of 0.81 grams more seed than the susceptible plants. This difference is more than ten times its probable error and is about 37 per cent of the mean yield of the resistant plants. In the open-panicled plants of the Minota-White Russian cross, the average yield of the susceptible plants is 0.23 grams less than of the resistant plants. The difference is about 12 per cent of the average yield of the resistant plants and is 2.9 times the probable error.

TABLE XIV

FREQUENCY DISTRIBUTIONS OF YIELD IN RELATION TO RUST REACTION IN THE OPEN-PANICLED TYPE OF THE F_2 GENERATION OF CERTAIN OAT CROSSES, GROWN IN 1921

Name	Rust class	Yield classes in grams														Total	Mean	Diff/ P. E.
		0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25	6.75			
Victory-White Russian	Re	23	41	42	41	58	43	35	18	11	8	2	..	2	1	325	2.17±0.05	....
Victory-White Russian	Su	14	28	30	11	5	5	4	4	1	..	..	..	1	..	102	1.36±0.06	10.1
Minota-White Russian	Re	71	67	78	69	55	55	47	30	15	9	5	2	..	1	504	1.94±0.04	....
Minota-White Russian	Su	20	26	23	27	16	12	6	6	3	1	3	..	..	..	143	1.71±0.07	2.9

TABLE XV

FREQUENCY DISTRIBUTIONS OF YIELD IN RELATION TO RUST REACTION IN THE SIDE-PANICLED TYPE OF THE F_2 GENERATION OF CERTAIN OAT CROSSES, GROWN IN 1921

Name	Rust class	Yield classes in grams														Total	Mean	Diff/ P. E.
		0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25	6.75			
Victory-White Russian	Re	7	4	8	8	8	6	1	..	1	1	..	..	..	..	53	2.04±0.11	....
Victory-White Russian	Su	3	9	4	6	2	1	..	..	1	1	..	..	..	..	32	1.56±0.12	3.0
Minota-White Russian	Re	12	13	11	4	7	6	1	3	..	1	..	..	..	..	72	1.94±0.11	....
Minota-White Russian	Su	5	3	5	..	..	1	1	..	..	..	..	..	..	..	20	1.28±0.14	3.7

Results in the side-panicled forms (Table XV) were similar to those obtained in the open-panicled forms. In the Victory-White Russian and Minota-White Russian crosses the differences between mean yields of resistant and susceptible plants are respectively 3.0 and 3.7 times the probable errors. In the first cross the difference is approximately 24 per cent of the average yield of the resistant plants and in the second cross the difference is approximately 34 per cent of the average yield of the resistant plants. In both crosses the rust resistant plants gave the greater average yields.

TABLE XVI

AVERAGE YIELDS OF THE F_2 GENERATION OF CERTAIN OAT CROSSES GROWN IN 1921

Name	Panicle type	Rust class	No. of plants	Average yield	Diff/ P. E.
Victory-White Russian	open	Re	325	2.17 ± 0.05	
Victory-White Russian	side	Re	53	2.04 ± 0.11	1.1
Victory-White Russian	open	Su	102	1.36 ± 0.06	
Victory-White Russian	side	Su	32	1.56 ± 0.12	1.5
Minota-White Russian	open	Re	504	1.94 ± 0.04	
Minota-White Russian	side	Re	72	1.94 ± 0.11	
Minota-White Russian	open	Su	143	1.71 ± 0.07	
Minota-White Russian	side	Su	20	1.28 ± 0.14	2.7

From the data presented in Tables XIV and XV a comparison may be made of the average yields of F_2 plants with the same parentage and of the same rust reaction but different with respect to panicle type. To facilitate such a comparison Table XVI has been prepared. Among the resistant F_2 plants of the Victory-White Russian cross the open-panicled forms yielded on the average 0.13 grams more than the side-panicled forms. This difference is only 1.1 times the probable error. Among the susceptible F_2 plants of the same cross the average yield of the side-panicled forms was 0.20 grams more than of the open-panicled forms, a difference 1.5 times its probable error and therefore not significant. The average yields of the open- and side-panicled F_2 resistant plants of the Minota-White Russian cross were the same. Among the susceptible individuals of the same cross, 20 side-panicled forms gave an average yield of 1.28 ± 0.14 grams, while 143 open-panicled forms gave an average yield of 1.71 ± 0.07. The difference is about 25 per cent of the mean yield of the open-panicled plants and is 2.7 times the probable error. The odds are about 14 to 1 against the chance of such a difference being due solely to random sampling. However, the number of plants in the side-susceptible group is too small to constitute a very desirable random sample. Considering all the differences between groups of like rust reaction but unlike panicle type, no consistent correlation between panicle type and yield was found.

The F_3 families homozygous for resistance to rust but segregating for panicle type are shown in Table XVII. By using only the segregating families, each plot is represented by the two classes of plants, i. e., open resistant and side resistant. This tends to minimize the possible effect of soil heterogeneity on the relative difference between the two classes. The data from which Table XVII was prepared may be found in the appendix (Tables XXXI, XXXII, XXXIIII, and XXXIV). The mean yield of the open-panicled forms did not differ significantly from the mean yield of the side-panicled forms in the Minota-White Russian cross. However, the Victory-White Russian cross showed a difference 5.1 times the probable error between the average yields of the two panicle types. This difference is about 22 per cent of the mean yield of the open-panicled plants, the higher yielding class, and can scarcely be attributed to chance.

The frequency distributions of the individual plant yields of F_3 families homozygous for both rust resistance and panicle type are shown in Table XVIII. The difference between the mean yield of open- and side-panicled forms is significant in both crosses. In one case the difference is 7.7· and in the other 5.5 times the respective probable errors. The mean yield of the side-panicled forms of the Minota-White Russian cross is about 73 per cent of the mean yield of the open-panicled forms. In the Victory-White Russian cross the mean yield of the side-panicled forms is about 78 per cent of what it is in the open-panicled forms.

AVERAGE YIELDS OF PARENTS

The number of plants harvested, their bulk yields, and the average yields per plant per plot are given in Tables XXXV and XXXVI, of the appendix. In Table XIX the frequency distributions of the average yield per plant per plot and the probable error of the average yield of a single plot of the Minota and Victory parents are shown. In the last column of the table the average number of plants per plot is given. Both the frequency distributions and the probable errors of the average plant yield of a single plot show that the soil in that part of the nursery used to grow the Minota parent and the Minota-White Russian F_3 families was more heterogenous than the part used to grow the Victory parent and the Victory-White Russian F_3 families. The mean yield of Victory was about 65 per cent of the mean yield of Minota. Owing to the fact that Minota matures somewhat earlier than Victory it is likely that stem rust reduced the yield of the latter more than of the former. The difference in yield between the parents may of course also be partly due to a difference in the productivity of the soil in the two parts of the nursery.

TABLE XVII

FREQUENCY DISTRIBUTIONS OF YIELD OF INDIVIDUAL PLANTS IN RELATION TO PANICLE TYPE IN F₃ FAMILIES SEGREGATING FOR PANICLE TYPE BUT RESISTANT TO RUST

Name	Culture No.	Panicle type	Yield classes in grams													Total	Mean	Diff/P. E.
			0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25			
Segregating for panicle type																		
Mimota x White Russian...........	4-4, etc.	open	13	27	49	49	35	24	21	7	4	2	2	2		235	1.95±0.05	....
Mimota x White Russian...........		side	7	16	20	11	17	12	8	3	0	1	1			96	1.84±0.07	1.2
Victory x White Russian and reciprocal	3-1, etc. and 2-2, etc.	open	11	32	35	44	29	25	21	13	9	4	0	1		224	2.06±0.05	....
Victory x White Russian and reciprocal		side	7	15	12	9	9	7	5	0	0	1				65	1.60±0.08	5.1

TABLE XVIII

FREQUENCY DISTRIBUTIONS OF YIELD OF INDIVIDUAL PLANTS IN RELATION TO PANICLE TYPE IN F₃ FAMILIES HOMOZYGOUS FOR BOTH RESISTANCE AND PANICLE TYPE

Name	Culture No.	Panicle type	Yield classes in grams													Total	Mean	Diff; P. E.
			0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25			
Homozygous for panicle type																		
Mimota x White Russian	4-4, etc.	open	22	33	47	48	40	24	21	11	9	6	4	1	1	267	2.02±0.05	....
Mimota x White Russian		side	28	34	34	37	16	10	7	6	1	1	1			174	1.48±0.05	7.7
Victory x White Russian and reciprocal	3-1, etc. and 2-2, etc.	open	11	10	21	23	30	21	18	9	7	0	4	2	1	168	2.49±0.07	....
Victory x White Russian and reciprocal		side	2	16	19	17	13	6	8	8	2	0	2			91	1.94±0.07	5.5

TABLE XIX

FREQUENCY DISTRIBUTIONS OF AVERAGE YIELD PER PLANT PER PLOT OF THE MINOTA AND VICTORY
PARENTS GROWN WITH THE F_3 FAMILIES IN 1921

Name	Average yield classes in grams							Total No. of plots	Mean	P. E. of Av. plant yield of a single plot	Av. No. of plants per plot
	0.625	0.875	1.125	1.375	1.625	1.875	2.125				
Minota.......	0	1	3	4	6	4	3	21	1.59 ± 0.05	grams 0.235	38.2
Victory.......	1	9	8	2	1	0	0	21	1.04 ± 0.03	0.151	33.9

Among the F_3 generations the White Russian parent appeared in
five systematically distributed plots. (Appendix Tables XXXV and
XXXVI). The average yields per plant per plot were 1.86, 1.98, 2.25,
2.37, and 1.98 grams, respectively, with a mean yield of 2.09 grams.
This mean yield is higher than the mean yields of the two open-
panicled parents.

AVERAGE YIELDS IN MINOTA-WHITE RUSSIAN AND VICTORY-WHITE RUSSIAN F_3 FAMILIES

Before yields of the F_3 families, which were harvested by the indi-
vidual plant method, could be compared with yields of the F_3 families
harvested in bulk, it was necessary to make a correction. Yields of a
few individual plants from each F_3 family harvested by the individual
plant method were determined in two ways. First the yield of each
plant was determined and then the seed from these plants was bulked
and the weight of this bulk seed ascertained. This procedure was fol-
lowed for each of the homozygous resistant F_3 families of which indi-
vidual plant yields were determined. The data and the correction
factor for each cross are shown in Table XX. The corrected total
and average yields are indicated in Tables XXXV and XXXVI of the
appendix. The apparent difference in yields by the two methods is
owing to the fact that the smaller quantities of seed obtained from
single plants were on the average underweighed by the balance used.

TABLE XX
DATA FROM WHICH CORRECTION FACTORS WERE COMPUTED

Name	Culture number	Number of plants	Yield in grams		Correction factor
			Sum of individual plant yields	Bulk yield	
Minota x White Russian.............	4-4, etc.	266	246.8	260.8	1.056
Victory x White Russian............. and reciprocal..................	3-1, etc. and 2-2, etc.	171	185.6	201.1	1.084

In Tables XXI and XXII are shown the frequency distributions for average yield per plant per plot of all the F_3 families in the Minota-White Russian and Victory-White Russian crosses, respectively. The frequency distributions are grouped according to the breeding nature of the F_3 families as are indicated in the three columns at the left in each table. The braces include the plant classes found in each plot. For example, the first four frequency distributions of each table are made up of plots segregating for both panicle type and rust reaction; hence with few exceptions there are open-panicled resistant and susceptible plants and side-panicled resistant and susceptible plants in each plot shown here. The mean yield of each category of plants and differences in terms of the probable errors between mean yields are shown at the right of each table. The average number of plants per plot and the probable error of the average plant yield of a single plot are recorded in the last two columns of the tables.

It will be observed, as shown in the tables, that certain frequency distributions have been combined and the mean yields and probable errors computed from these combined distributions. Such a procedure in the open-panicled susceptible, and side-panicled resistant, groups necessitated combining distributions representing considerable differences in the average number of plants per plot. However, in view of the general similarity between the two distributions combined in each case, and the magnitude of the probable error of the yield of a single plot based on an average of approximately seven plants, this method was used altho not wholly justified from a mathematical standpoint. As is expected, the magnitude of the probable error of the average plant yield of a single plot is generally less where a relatively large number of plants make up the average yield than where but a few plants make up the average yield. Nevertheless the probable errors of yields of single plots indicate that an average yield based on seven plants is almost as trustworthy as an average yield based on twenty plants.

The last four frequency distributions of each of the tables are made up from the F_3 families homozygous for both panicle type and rust reaction. The probable errors of the means in these cases are calculated from a probable error of a single determination of somewhat greater magnitude than was actually found in any frequency distribution comprising average yields based on twenty or more plants. This arbitrary method rather than a method suggested by Student (1908) was used owing to the differences in the number of F_3 families making up the various frequency distributions.

Considering first the Minota-White Russian cross (Table XXI), it is obvious that there are greater and more significant differences

between the mean yields of plants with like panicle type but unlike rust reaction than there are between the mean yields of plants with unlike panicle type but like rust reaction. In the former the differences between mean yields are 4.8, 0.5, 6.1, 5.2, 3.3, and 1.1 times their respective probable errors; whereas in the latter the differences in mean yields are 0.1, 3.9, 0.4, 0.6, 2.9, and 0.4 times their respective probable errors. In all cases the average yield of the resistant plants was greater than the average yield of the susceptible plants of the same panicle type altho in two instances the differences are not significant. Among the average yields of plants with like rust reaction but unlike panicle type there were two cases where open-panicled resistant plants gave significantly greater yields than side-panicled resistant plants. On the average, reaction to stem rust had more influence on yield than panicle type. The average yield per plot of the open panicled susceptible plants is about 76 per cent of that in the open-panicled resistant plants, whereas among the side-panicled forms the average yield per plot of the susceptible plants is about 86 per cent of that in the resistant plants.

In the Victory-White Russian cross (Table XXII) the data show that susceptibility to rust reduced the yield even more than in the Minota-White Russian cross. On the other hand no highly significant difference was found between mean yields of plants with like rust reaction but unlike panicle type. The differences between mean yields based on rust reaction are 7.0, 5.5, 7.8, 4.4, 8.4, and 4.0 times the respective probable errors and the differences between mean yields based on panicle type are 0.1, 1.0, 0.9, 1.4, 0.4, and 2.3 times the respective probable errors. In the former case the differences are all significant and in the latter case none is significant with one possible exception. The average yield per plot of the open-panicled susceptible plants is approximately 63 per cent of that in the open-panicled resistant plants and among the side-panicled forms the average yield per plot of the susceptible plants is about 70 per cent of that in the resistant plants. On the average the F_3 families of the Victory-White Russian cross were later in maturing than those of the Minota-White Russian cross. This fact undoubtedly accounts at least in part for the apparently greater effect of rust in reducing yield in the Victory-White Russian F_3 families.

TABLE XXI

FREQUENCY DISTRIBUTIONS OF AVERAGE YIELD PER PLANT PER PLOT OF THE MINOTA-WHITE RUSSIAN F₃ FAMILIES (CULTURES 44, ETC.) GROWN IN 1921

F₃ families	Panicle type	Rust class	0.375	0.625	0.875	1.125	1.375	1.625	1.875	2.125	2.375	2.625	2.875	3.125	Total number of plots	Mean	Rust class Diff./ P.E.	Panicle type Diff./ P.E.	Av. No. of plants per plot	P.E. of Av. plant yield of a single plot
																			grams
Segregating for both panicle type and rust reaction.......	open	Re			1	1	2	3	5	6	3	4			23	2.06±0.05		0.1	22.4	0.255
	open	Su	1		1	2	2	3	7	4	1	1	1		23	1.68±0.06	4.8	3.9	7.0	0.302
	side	Re	1		1		7	5	4	4	1	1	1	1	23	1.75±0.06			7.2	0.298
	side	Su	1	2	2	2	5	2	2	2	3		1		23	1.69±0.09	0.5		2.7	0.408
Homozygous open, segregating for rust......	open	Re			1	1	1	1	3	2		1			10	⟩ a,b			27.9	.....
	open	Su		2	1	1	3	3							10				9.3	.....
Homozygous side, segregating for rust......	side	Re			1		2	1	1	2	1	1			9	⟩ c,d			26.7	.....
	side	Su			1	1	4	2							9				9.1	.....
Homozygous resistant, segregating for panicles......	open	Re					2	3	4	1	1	1		1	11	1.90±0.07a			24.0	0.324
	side	Re					4	4	2	1				1	11	1.86±0.08c		0.4	9.6	0.352
Homozygous susceptible, segregating for panicles......	open	Su				1	7	3	1					⁊	12	1.35±0.05b	6.1		28.7	0.209
	side	Su		2		3	2	5							12	1.39±0.05d	5.2	0.6	8.6	0.230
Open resistant.......							2	1	1	2			1		10	2.08±0.11*			30.4	.....
Open susceptible.......					1	1	2	1							4	1.38±0.18*	3.3		38.8	.....
Side resistant.......						1	1	2	1						5	1.53±0.16*		2.9	34.8	.....
Side susceptible.......					1	1	2	1							5	1.28±0.16*	1.1	0.4	39.4	.....

a, b, c, d. Frequency distributions marked with the same letter were combined before calculating the constants.
* Probable error calculated on the basis of 0.350 as the probable error of a single determination.

TABLE XXII

FREQUENCY DISTRIBUTIONS OF AVERAGE YIELD PER PLANT PER PLOT OF THE VICTORY-WHITE RUSSIAN F_3 FAMILIES
(CULTURES 3-1, ETC. AND 2-2, ETC.), GROWN IN 1921

F_3 families	Panicle type	Rust class	Average yield classes n grams 0.375	0.625	0.875	1.125	1.375	1.625	1.875	2.125	2.375	2.625	2.875	3.125	3.375	3.625	3.875	Total number of plots	Mean	Rust class Diff/P.E.	Panicle type Diff/P.E.	Av. No. of plants per plot	P.E. of Av. plant yield of a single plot
Segregating for both panicle type and rust reaction	open	Re			1	1	3	3	7	6	8	3	2	1				35	2.08 ± 0.06			19.5	grams 0.337
	open	Su	1	3	1	9	6	8	7	2	2				1			35	1.45 ± 0.07	7.0	0.1	7.2	0.372
	side	Re				1	1	8	2	2	4	3	3		1			35	1.99 ± 0.07		1.0	4.8	0.383
	side	Su		5	5	6	1	5	5	5	2	1		2				33	1.44 ± 0.07	5.5		3.2	0.403
Homozygous open, segregating for rust	open	Re					1	2	3	1	3		1	1				10	a			23.2	
	open	Su	1		4	2		1				1		2				10	b			9.5	
Homozygous side, segregating for rust	side	Re					1		1	2	1	1						6	c			26.0	
	side	Su			2	2	4	2	1									6	d			7.7	
Homozygous resistant, segregating for panicles	open	Re					1	3	1	1	2	1	1	1				11	$2.05\pm0.07a$			22.3	0.317
	side	Re					4		1	2	2			1				11	$1.95\pm0.09c$		0.9	6.5	0.355
Homozygous susceptible, segregating for panicles	open	Su			1	5	1	4	1									12	$1.27\pm0.07b$	7.8		22.2	0.308
	side	Su	1	1	2	1	2	2		4								12	$1.42\pm0.08d$	4.4	1.4	7.7	0.334
Open resistant					1				1			1	1	1	1		1	6	$2.67\pm0.14*$			28.0	
Open suscep'ble				2	1	2	1	1	1									8	$1.16\pm0.12*$	8.4	0.4	34.4	
Side resistant								1	1				1					3	$2.13\pm0.20*$		2.3	30.3	
Side susceptible					1	3	4											8	$1.23\pm0.12*$	4.0		37.0	

a, b, c, d. Frequency distributions marked with the same letter were combined before calculating the constants.
* Probable error calculated on the basis of 0.350 as the probable error of a single determination.

DISCUSSION

The difference in the parasitic reaction of the pure line hosts, Victory, Minota, and White Russian oats to the fungus stem rust is because of physiological rather than morphological characters. The parasite gains admittance to all three oat varieties but does not develop equally well in all. A heavily infected White Russian plant manifests many small uredinia, whereas a Victory or Minota plant, under the same condition, manifests many large uredinia; in some cases considerable areas of the surface of the oat stem, particularly near the nodes, become entirely covered with rust spores. Resistance to rust is relative, not absolute.

The difference in host reaction to rust is a character definitely inherited. If Victory or Minota is crossed with White Russian, the F_2 generation consists of two kinds of plants, namely, resistant and susceptible. The reaction to rust of approximately three fourths of the F_2 plants is like that of the resistant parent and of one fourth like that of the susceptible parent. The F_2 plants produce three kinds of F_3 families. Seed from susceptible F_2 individuals gives rise to susceptible progeny, whereas seed from approximately one third of the resistant F_2 individuals produces resistant progeny, and seed from the other two thirds produces progeny which again show segregation in the ratio of three resistant to one susceptible plant. The difference in rust reaction between the parents is apparently due to a single factor difference.

Some evidence is also shown for assuming that a single main factor difference between the parents is operating in the inheritance of panicle type. The resistant parent is side-panicled and the susceptible parents are open-panicled forms. The segregation of the F_2 generation and the frequency with which side-panicled susceptible, and open-panicled resistant F_3 families are obtained indicate that rust reaction and panicle type are not closely linked in inheritance.

Yield of seed in oats is materially decreased by the action of stem rust. The two important characteristics of host plants which largely determine the extent of the decrease in yield are length of time required to mature and reaction to the parasitic fungus. Other things being equal, an early maturing variety of oats has a better chance to escape injurious rust infection than a later maturing variety. In the present investigation the extent of the decrease in yield of seed caused primarily by stem rust was measured. In nearly all cases the mean yield of resistant plants was significantly greater than the mean yield of similar plants but susceptible to rust. The genotypes of the plants compared differed of course in other respects than rust reaction, but the number

of plants on which yield determinations were made is sufficiently great to place considerable confidence in the results. It is of interest to note that the average reduction of yield because of rust is greater in the Victory-White Russian progeny than it is in the Minota-White Russian progeny. The former averaged somewhat later in maturing than the latter.

SUMMARY

1. Two open-panicled pure lines of oats, Minota and Victory, which are susceptible to stem rust, were crossed with a side-panicled pure line of White Russian oats which is relatively resistant to stem rust. The inheritance of host reaction to rust, panicle type, and pollen abortion were studied in the F_1, F_2, and F_3 generations. A study was also made of the correlation between rust reaction and yield and between panicle type and yield during one of the three years the investigation was in progress.

2. The relative length and breadth of the stomata through the guard cells on the under surface of the leaves of nearly matured plants of the Victory and White Russian oat strains used in this investigation indicate that the rust resistance of White Russian is not owing to relative size of stomata. This conclusion was corroborated by the relative width of the stomatal openings when at a maximum in the seedlings of the same varieties.

3. Rust resistance is inherited as a dominant character depending on a single factor difference for its expression. In both crosses, Minota-White Russian and Victory-White Russian, 3044 F_2 plants and 377 F_3 families were examined for their reaction to rust. In all, the F_2 generations consisted of 2340 resistant and 704 susceptible plants. Of the F_3 families, 106 bred true for resistant, 175 segregated in the ratio of three resistant to one susceptible plant, and 96 bred true for susceptibility. The segregating F_3 families produced 5964 resistant and 1970 susceptible plants.

4. In the above crosses panicle type is dependent on a single main factor for its expression. The F_1 plants were open-panicled but not to the same degree as the open-panicled parents. In all the F_3 families of both crosses there were 98 homozygous open, 213 showing segregation, and 66 homozygous side.

5. Evidence is presented which indicates that panicle type and rust reaction are nearly, if not completely, independent in their inheritance.

6. The Victory parent produced on the average 12.4 per cent aborted pollen. Minota and White Russian produced on the average 1.0 and 0.9 per cent aborted pollen, respectively. In the Victory-White

Russian cross of 250 F_2 plants, 7 produced percentages of aborted pollen within the range exhibited by the Victory parent.

7. In 1921 the F_2 and F_3 generations were analyzed to determine the potency of rust in reducing yield of seed. In the F_2 generations the approximate average reduction of yield because of rust in the Minota-White Russian cross was 12 per cent among the open-panicled forms and 34 per cent among the side-panicled forms; and in the Victory-White Russian cross 37 per cent among the open panicled plants and 24 per cent among the side-panicled plants; in the F_3 generations the average percentage reductions of yield were 24, 14, and 37, 30 in the two crosses, respectively.

8. The correlation between panicle type and yield was not consistent. However, in every instance where a significant difference was found, the open-panicled forms gave the greater average yields. The approximate percentage differences between average yields of all the plants of the same parentage and rust reaction but different panicle type are given below. Percentages are based on the average yield of the open-panicled type in each case. Considering first the plants harvested individually, the resistant open-panicled plants of the Victory-White Russian cross yielded 16 per cent more than the resistant side-panicled plants. Among the susceptible plants of the same cross, the side-panicled type yielded 15 per cent more than the open-panicled type. In the Minota-White Russian cross the average yield of the open-panicled resistant forms exceeded that of the side-panicled resistant forms by 14 per cent, whereas among the susceptible plants, forms with open panicles yielded on the average 25 per cent more than forms with side panicles. Considering the bulk yields, differences also appear. Of the two panicle types in the Minota-White Russian cross, the open-panicled type gave the greater average yield (12 per cent) among the resistant plants and the side-panicled type gave slightly the greater average yield (about 1 per cent) among the susceptible plants. In the Victory-White Russian cross, the open-panicled resistant plants yielded 7 per cent more and the side-panicled susceptible plants 4 per cent more than the plants of the same rust reaction but of different panicle type.

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APPENDIX

TABLE XXIII

White Russian x Victory F₃ Progenies, Grown in 1920, Showing Rust Reaction and Panicle Type

Culture number	No. of plants*		Panicle type†			Culture number	No. of plants*		Panicle type†		
	Re	Su	O	H	S		Re	Su	O	H	S
2-13- 1	35	17			x	2-13-21	72			x	
2-13- 2	62	16			x	2-13-22	15	6			x
2-13- 3		21		x		2-13-23	83			x	
2-13- 4		21		x		2-13-24	64			x	
2-13- 5		21		x		2-13-25	44			x	
2-13- 6			x	x		2-13-26	13				x
2-13- 7	77	17		x		2-13-27			x		
2-13- 8	68			x		2-13-28	13	19		x	
2-13- 9	73			x		2-13-30	12	5		x	
2-13-10		20		x		2-13-31	15			.	
2-13-11		31		x		2-13-32	35	12	x		
2-13-12	55				x	2-13-33		20	x		
2-13-13	22			x		2-13-34		13	x		
2-13-14	19	22		x		2-13-35			x		
2-13-15	59			x		2-13-36	13	3			
2-13-16	58	18		x		2-13-37	11	9	x	x	
2-13-17	65		x	x		2-13-38	24			x	
2-13-18	52	19		x	x	2-13-39	27				
2-13-19	78					2-13-40	16			x	
2-13-20	79	19	x		x	2-13-41	17	2	x		x
		41					6				

*Re = resistant; Su = susceptible.   †O = open; H = segregating; S = side.

TABLE XXIV

WHITE RUSSIAN x VICTORY F₃ PROGENIES, GROWN IN 1921, SHOWING RUST REACTION AND PANICLE TYPE

Culture number	No. of plants*		Panicle type†			Culture number	No. of plants*		Panicle type†		
	Re	Su	O	H	S		Re	Su	O	H	S
2-2- 1	11	22				2-2-26	21	10	x	x	
2-2- 2	27	5		x		2-2-27		32			x
2-2- 3	30	9		x		2-2-28		6			x
2-2- 4	32		x			2-2-29		41			
2-2- 5	31	10		x		2-2-30	30	36			
2-2- 6	27	10	x			2-2-31		15			
2-2- 7	27			x		2-2-32				x	
2-2- 8	34			x		2-2-33	22	33		x	x
2-2- 9	25	10	x			2-2-34	29				
2-2-10		24				2-2-35					
2-2-11	33	7			x	2-2-36	29	9	x	x	
2-2-12		34		x		2-2-37	30		x		
2-2-13	26	26		x	x	2-2-38	26	8	x	x	
2-2-14	5	7			x	2-2-39	18	9		x	
2-2-15	24	24		x		2-2-40	29			x	
2-2-16		36			x	2-2-41	24	7		x	
2-2-17		41			x	2-2-42	27	26		x	
2-2-18		13				2-2-43	23	11		x	
2-2-19	24	9		x		2-2-44	13	11		x	
2-2-20	23				x	2-2-45		7		x	
2-2-21	27	11		x		2-2-46	17	6		x	
2-2-22	28	11		x		2-2-47	20	6	x	x	
2-2-23	31	8		x		2-2-48	29	7			x
2-2-24	23	6	x	x		2-2-49	25	10		x	
2-2-25	25					2-2-50	17	39			x
							26				x

*Re =resistant; Su =susceptible. †O =open; H =segregating; S =side.

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TABLE XXV

White Russian x Victory F$_3$ Progenies, Grown in 1921, Showing Rust Reaction and Panicle Type

Culture number	No. of plants*		Panicle type†			Culture number	No. of plants*		Panicle type†		
	Re	Su	O	H	S		Re	Su	O	H	S
3-1- 1	29	....	x			3-1-26	....	36	x		x
3-1- 2	....	39	x			3-1-27	21	7		x	
3-1- 3	....	13		x		3-1-28	19	14		x	
3-1- 4	11	....			x	3-1-29	....	31		x	
3-1- 5	36	....			x	3-1-30	....	7			
3-1- 6	23	6		x		3-1-31	....	9			
3-1- 7	....	33	x			3-1-32	27	41	x		
3-1- 8	....	20	x			3-1-33	26	17	x		
3-1- 9	25	7			x	3-1-34	....	38		x	
3-1-10	....	42		x		3-1-35	15	36	x		
3-1-11	31	....		x		3-1-36	....	34	x		
3-1-12	28	8		x		3-1-37	....	7	x		
3-1-13	....	35		x		3-1-38	31	6		x	
3-1-14	28	12		x		3-1-39	34	34		x	
3-1-15	29	8		x		3-1-40	....	11		x	
3-1-16	30	....			x	3-1-41	....	7		x	
3-1-17	....	37		x		3-1-42	24	....		x	
3-1-18	27	....		x		3-1-43	25	8		x	
3-1-19	21	6		x		3-1-44	30	6		x	
3-1-20	27	....	x			3-1-45	27	....		x	
3-1-21	....	31		x		3-1-46	30	....	x		x
3-1-22	26	6	x			3-1-47	29	....		x	
3-1-23	33	7	x	x		3-1-48	31	11		x	
3-1-24	19	15		x		3-1-49	16	5	x	x	
3-1-25	....	36		x		3-1-50	29	32		x	

*Re = resistant; Su = susceptible.   †O = open; H = segregating; S = side.

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TABLE XXVI

MINOTA × WHITE RUSSIAN F₃ PROGENIES, GROWN IN 1920, SHOWING RUST REACTION AND PANICLE TYPE

Culture number	No. of plants* Re	No. of plants* Su	Panicle type† O	Panicle type† H	Panicle type† S
4-7- 1	73			x	
4-7- 2		21			x
4-7- 3	68		x	x	
4-7- 4	32	6			x
4-7- 5	73	14			x
4-7- 6	82			x	
4-7- 7	66	19		x	
4-7- 8	64	13		x	
4-7- 9		45	x		
4-7-10	82				
4-7-11	19	35		x	
4-7-12				x	
4-7-13				x	
4-7-14	79	6	x		
4-7-15	29	13		x	
4-7-16	67	21	x		
4-7-17					
4-7-18	76	14		x	
4-7-19	73	23		x	
4-7-20	56			x	
4-7-21	64	21	x		
4-7-22	59		x	x	
4-7-23	18			x	
4-7-24		8			x
4-7-25	31	17		x	
4-7-26	40				
4-7-27	70	16	x	x	
4-7-28	76	12		x	
4-7-29	72	14			
4-7-30	33	25	x	x	
4-7-31	66	13	x		
4-7-32		12		x	
4-7-33	66			x	
4-7-34	52			x	
4-7-35	88	15			x
4-7-36				x	
4-7-37	68			x	
4-7-38		76	x		
4-7-39		73		x	
4-7-40	16	3		x	
4-7-41	64	20		x	
4-7-42	60	7			
4-7-43	6	2			
4-7-44				x	
4-7-45	72	21		x	x

*Re = resistant;   Su = susceptible.   †O = open;   H = segregating;   S = side.

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TABLE XXVII

MINOTA ×WHITE RUSSIAN F₃ PROGENIES, GROWN IN 1920, SHOWING RUST REACTION AND PANICLE TYPE

Culture number	No. of plants*		Panicle type†			Culture number	No. of plant*		Panicle type†		
	Re	Su	O	H	S		Re	Su	O	H	S
4-8- 1	...	19		x		4-8-26						
4-8- 2	...	19		x		4-8-27	54	24	x		
4-8- 3	...	20		x		4-8-28	69	...			
4-8- 4	...	21		x		4-8-29	...	19			
4-8- 5	64	20		x		4-8-30	76	...			
4-8- 6	55	18			x	4-8-31	64	23			
4-8- 7						4-8-32	68	16			
4-8- 8	74	17		x		4-8-33	60	21			
4-8- 9	58	8		x		4-8-34	82	...	x		
4-8-10	4	...	x			4-8-35	55	21	x		
4-8-11	33	...	x			4-8-36	54	27	x		
4-8-12	23	21	x	x		4-8-37	...	21			
4-8-13		14		x		4-8-38	59	18		x	
4-8-14	55	...	x			4-8-39	66	12			
4-8-15	81	5	x			4-8-40	43	...	x	x	
4-8-16	16	19	x			3-8-41	80	...		x	
4-8-17	...	38	x		x	4-8-42	71	19		x	
4-8-18	76	...	x		x	4-8-43					
4-8-19	19	...				4-8-44	70	25	x	x	
4-8-20	57	...	x		x	4-8-45	51	...		x	
4-8-21		26				4-8-46	90	...		x	
4-8-22	67	16		x		4-8-47				x	
4-8-23	...	18		x		4-8-48	68	22		x	
4-8-24	...	22	x			4-8-49	67	17		x	
4-8-25	...	18	x			4-8-50	75	24	x	x	
							...	19		x	

*Re = resistant;   Su = susceptible.   †O = open;   H = segregating;   S = side.

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TABLE XXVIII

MINOTA x WHITE RUSSIAN F₃ PROGENIES, GROWN IN 1920, SHOWING RUST REACTION AND PANICLE TYPE

Culture number	No. of plants* Re	Su	Panicle type† O	H	S
4-9- 1	....	18			
4-9- 2	15	6		x	x
4-9- 3	....	22			
4-9- 4	70	16		x	
4-9- 5	14	5		x	
4-9- 6	18	....			x
4-9- 7	76	....			x
4-9- 8	....	33	x	x	
4-9- 9	57	21		x	
4-9-10	39	25			
4-9-11	36	10		x	
4-9-12	....	....			
4-9-13	12	20		x	x
4-9-14	40	5		x	
4-9-16	....	6		x	
4-9-18	13	19		x	
4-9-19	65	4		x	
4-9-20	....	....	x		
4-9-21	80	16	x		
4-9-22	82	....			
4-9-23	17	....	x	x	
4-9-24	28	3	x		

Culture number	No. of plants* Re	Su	Panicle type† O	H	S
4-9-25	19	....			x
4-9-26	....	18	x		
4-9-27	28	6	x		
4-9-28	26	8		x	
4-9-29	10	....	x		
4-9-31	43	29			
4-9-32	42	....		x	
4-9-33	84	....		x	
4-9-34	55	....		x	
4-9-35	64	24			
4-9-36	45	15	x	x	
4-9-38	64	10		x	
4-9-39	63	17	x	x	
4-9-40	10	....			
4-9-41	53	3	x		
4-9-42	9	16	x		
4-9-43	20	1			
4-9-44	....	....			
4-9-45	51	17	x	x	
4-9-46	7	11			
4-9-47	15	3		x	x

*Re = resistant; Su = susceptible. †O = open; H = segregating; S = side.

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TABLE XXIX

Minota x White Russian F₃ Progenies Grown in 1921, Showing Rust Reaction and Panicle Type

Culture number	No. of plants* Re	No. of plants* Su	Panicle type† O	Panicle type† H	Panicle type† S
4-4-1	28			×	
4-4-2	32	3		×	
4-4-3	30	4		×	
4-4-4	36		×		
4-4-5	28	6		×	
4-4-6	28			×	
4-4-7	38				×
4-4-8	25	10	×		
4-4-9	35	5	×		
4-4-10	29	8	×	×	
4-4-11	28	11	×		
4-4-12	23	15		×	
4-4-13	37			×	
4-4-14	24	12		×	
4-4-15	24	13		×	
4-4-16	33	12	×		
4-4-17	20	12	×	×	
4-4-18	32			×	
4-4-19	19		×	×	
4-4-20	30	37	×		
4-4-21				×	×
4-4-22	26	37		×	×
4-4-23	30	10			
4-4-24	27				
4-4-25	30	6		×	
4-4-26	29	6			
4-4-27		4	×		
4-4-28	9	40		×	
4-4-29	31				
4-4-3	2	12		×	
4-4-31		1		×	
4-4-32		43		×	
4-4-33	33	37		×	
4-4-34		29	×		
4-4-35		10		×	
4-4-36	29	38		×	
4-4-37		9			
4-4-38		35		×	
4-4-39	37	6		×	
4-4-40	28		×		
4-4-41	37	6		×	
4-4-42	28				
4-4-43		30			
4-4-44	31	6			
4-4-45		37			
4-4-46		4			
4-4-47	31	37			
4-4-48		7			
4-4-49	27	43			
4-4-50			×		
4-4-51	25	9	×		
4-4-52	28	12	×		
4-4-53	25	7			
4-4-54	29	15			
4-4-55	26	41			
4-4-56		38			
4-4-57	28	16	×		
4-4-58	21	8			
4-4-59	33	8			
4-4-60		42			
4-4-61		34		×	
4-4-62	27			×	
4-4-63		34			
4-4-64	25	7		×	
4-4-65	31	11		×	
4-4-66		40		×	
4-4-67	39			×	
4-4-68	23	7		×	
4-4-69	39			×	
4-4-70	29			×	
4-4-71	35	12		×	
4-4-72		6		×	
4-4-73		35		×	
4-4-74	30	31		×	
4-4-75	35	8		×	
4-4-76	27				
4-4-77	31	13		×	
4-4-78	35	10	×	×	

*Re = resistant; Su = susceptible. †O = open; H = segregating; S = side.

TABLE XXIX—*Continued*

Minota x White Russian F_3 Progenies Grown in 1921 Showing Rust Reaction and Panicle Type

Culture number	No. of plants*		Panicle type†			Culture number	No. of plants *		Panicle type†		
	Re	Su	O	H	S		Re	Su	O	H	S
4-4-79	38	....				4-4-90	....	39	x		
4-4-80	29	11				4-4-91	23	11			
4-4-81	35	....		x	x	4-4-92	37	....	x	x	x
4-4-82	35	....		x	x	4-4-93	....	38			x
4-4-83	37	....	x			4-4-94	20	5			
4-4-84	....	35	x			4-4-95	39	....			
4-4-85	25	10	x		x	4-4-96	32	9		x	
4-4-86	31	....	x			4-4-97	34	8		x	
4-4-87	31	....	x			4-4-98	....	42		x	
4-4-88	35	8		x		4-4-99	32	....	x		
4-4-89	29	10			x	4-4-100	29	8			x

*Re =resistant; Su =susceptible.   †O =open; H =segregating; S =side.

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TABLE XXX

Segregation of F_2 Plants with Respect to Rust Reaction and Panicle Type as Revealed by Their F_3 Progenies. (Tables XXIII to XXIX inclusive)

Name	Culture number	Year F_3 was grown	No. of F_2 plants								
			Homozygous resistant			Heterozygous resistant			Homozygous susceptible		
			Panicle type			Panicle type			Panicle type		
			Open	Segregating	Side	Open	Segregating	Side	Open	Segregating	Side
White Russian x Victory	2-13	1920	1	13	4	4	5	4	4	4	1
White Russian x Victory	2-2	1921	3	5	2	5	20	4	1	4	6
Victory x White Russian	3-1	1921	3	6	1	5	15	3	7	8	2
Minota x White Russian	4-7	1920	5	10	0	3	12	4	2	6	2
Minota x White Russian	4-8	1920	3	9	3	7	12	0	7	0	3
Minota x White Russian	4-9	1920	5	5	2	6	12	5	1	7	0
Minota x White Russian	4-4	1921	10	11	5	10	29	10	6	14	5

TABLE XXXI

FREQUENCY DISTRIBUTIONS OF INDIVIDUAL PLANT YIELD IN OPEN-PANICLED, RUST-RESISTANT F₃ PROGENY OF MINOTA x WHITE RUSSIAN CROSS

Culture number	Yield classes in grams													Total number
	0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25	
4-4-1	1	7	2	6	2	1	-		1					20
4-4-4*	1	2	3	9	6	5	1	5	2	1	1			36
4-4-12	2	3	3	5	1	2	3	1						20
4-4-18*	2	4	2	4	4		1	1	1					19
4-4-20*	6	7	6	1	4	2	2			1	1			30
4-4-28		2	7	5	4	3								21
4-4-40*	2	4	8	5	4	2	1		2					28
4-4-42		4	6	7	2	1			1					21
4-4-50*	1	1	9	6	2	1	5							25
4-4-62	3		4	4	5	2	1	1						20
4-4-67	2	1	8	3	3	2	5	2	1	1	1			29
4-4-75		1	1	4	5	2	5	3		1	1	2		25
4-4-78*	3	2	6	5	7	6	4	1		1				35
4-4-81	1	4	8	4	4	4	3							28
4-4-82	3	3	5	6	4	1	2							24
4-4-86*	3	4	5	7	5	3	1	2				1		31
4-4-87*	1	3	3	4	3	5	3	2	3	3	1			31
4-4-95	1	2	5	5	5	6	2		1					27
4-4-99*	3	6	5	7	5		3		1		1		1	32

*Homozygous for panicle type.

TABLE XXXII

FREQUENCY DISTRIBUTIONS OF INDIVIDUAL PLANT YIELD IN SIDE-PANICLED, RUST-RESISTANT F₃ PROGENY OF MINOTA x WHITE RUSSIAN CROSS

Culture number	Yield classes in grams											Total number
	0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	
4-4-1	1	2	1	1	1	2						8
4-4-6*	7	8	6	7	5	4		1				38
4-4-12		2	6	5	2	1						16
4-4-17*	5	7	4	8	3		2	2				31
4-4-23*	2	7	7	7	2	2	3					30
4-4-28	1	3	2		2							8
4-4-42		2	2		1		2					7
4-4-62	1	1	4				1					7
4-4-67	1	2		1	2	4						10
4-4-75				1	2	2	3	1		1		10
4-4-79*	5	4	8	8	3	3	2	3	1	1		38
4-4-81	1	2	1	1	1		1					7
4-4-92*	9	8	9	7	3	1						37
4-4-95			2	1	4	2	1	1			1	12

*Homozygous for panicle type.

TABLE XXXIII

FREQUENCY DISTRIBUTIONS OF INDIVIDUAL PLANT YIELD IN OPEN-PANICLED, RUST-RESISTANT F_3 PROGENY OF VICTORY x WHITE RUSSIAN AND THE RECIPROCAL CROSSES

Culture number	Yield classes in grams													Total number
	0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25	
3-1-1*	1		2		5	4	3	1	3	5	3	2		29
3-1-10	1	2	1	5	6	4	3	2	1					25
3-1-15	5	6	4	4	2	2			3					24
3-1-17	1	2	3	5	4	2	3					1		21
3-1-19		2	3	2	4	6		2						19
3-1-42	1	2	1	5	3	5	8	1	1	1				28
3-1-45		2	3	2	3	1	2	1						14
3-1-46*	2	1	5	7	6	1	3	1	1	2		1	1	31
3-1-49*			2	7	5	4	5	3	2	1				29
2-2-4*		2	6		3	9	5	3	1	1	1		1	32
2-2-7	2	5	8	4	1									20
2-2-8		3	2	3	2	2	4	7	4	2				29
2-2-25		2	5	8	2	3								20
2-2-32	1	6	5	6	4		1			1				24
2-2-35*	4	3	3	8	7	2	2							29
2-2-37*	4	4	3	1	4	1		1						18

*Homozygous for panicle type.

TABLE XXXIV

FREQUENCY DISTRIBUTIONS OF INDIVIDUAL PLANT YIELD IN SIDE-PANICLED, RUST RESISTANT F_3 PROGENY OF VICTORY x WHITE RUSSIAN AND RECIPROCAL CROSSES

Culture number	Yield classes in grams										Total number
	0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	
3-1-4*	1	4	2	3	7	2	8	7	2		36
3-1-10		1		1	1	2	1				6
3-1-15		1	1	2	1	1					6
3-1-17		2	1	1			1			1	6
3-1-19	2	3			2	1					8
3-1-42						1	1				2
3-1-45	2	5	3	2	1	1	1				15
2-2-7	1	3	2		1	1	1				7
2-2-8			2	1	1	1					5
2-2-13*	1	6	4	8	4	2		1			26
2-2-25	2		1	1	1						5
2-2-32			2	1	1	1					5
2-2-34*		6	13	6	2	2					29

*Homozygous for panicle type.

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TABLE XXXV

PLANTING PLAN AND YIELDS OBTAINED IN THAT PART OF THE NURSERY USED TO GROW THE PARENTS AND THE MINOTA-WHITE RUSSIAN F₃ FAMILIES IN 1921. PARENTS AND PROGENY ARRANGED IN THE ORDER IN WHICH THEY APPEARED IN THE NURSERY

Culture number or parent	Open panicles — Resistant No. of plants	Total yield	Average yield	Open panicles — Susceptible No. of plants	Total yield	Average yield	Side panicles — Resistant No. of plants	Total yield	Average yield	Side panicles — Susceptible No. of plants	Total yield	Average yield
		grams	grams		grams	grams		grams	grams		grams	grams
White Russian				36	61.2	1.70	32	59.4	1.86			
Minota												
4-4-1	20	31.7†	1.59				8	13.2†	1.65			
4-4-2	Eliminated											
4-4-3	Eliminated											
4-4-4	36	94.0†	2.61									
4-4-5	Eliminated											
Minota*				32	27.9	0.87						
4-4-6	16	21.2	1.33				38	56.5†	1.49			
4-4-7	35	74.7	2.13	6	6.0	1.00	9	14.6	1.62	4	4.0	1.00
4-4-8	29	44.4	1.53	5	7.5	1.50						
4-4-9	20	53.5	2.68	8	5.7	0.71	8	14.2	1.78	4	7.0	1.75
4-4-10				7	18.8	2.69						
Minota				42	75.1	1.79						
4-4-11	23	44.7	1.94	15	24.8	1.65	16	26.4†	1.65			
4-4-12	20	38.5†	1.93	10	20.8	2.08	9	11.7	1.30	2	3.6	1.80
4-4-13	15	32.0	2.13	9	10.6	1.18	9	12.0	1.33	4	6.1	1.53
4-4-14	15	25.2	1.68	10	17.0	1.70	7	14.6	2.09	2	2.8	1.40
4-4-15	26	52.5	2.02	43	83.7	1.95						
Minota				12	15.1	1.26						
4-4-16	20	48.2	2.41	30	35.8	1.19	31	48.8†	1.57	7	7.0	1.00
4-4-17	19	35.1†	1.85									
4-4-18												
4-4-19	30	49.6†	1.65									
4-4-20												
Minota				45	77.6	1.72						
4-4-21	17	36.5	2.15	29	39.6	1.37	9	16.0	1.78	8	13.1	1.64
4-4-22				7	14.2	2.03	30	49.1†	1.64	3	5.1	1.70
4-4-23	Eliminated											
4-4-24	Eliminated											
4-4-25				36	36.3	1.01						
Minota*				40	59.5	1.49						
4-4-26							29	22.3	0.77	4	3.9	0.98
4-4-27												
4-4-28	21	38.3†	1.82				8	10.0†	1.25			
4-4-29	23	37.0	1.61	9	8.2	0.91	8	13.5	1.69	3	4.1	1.37
4-4-30	23	46.2	2.01	9	12.3	1.37	5	7.8	1.56	1	0.3	0.30

*Injured.   †Corrected yield (See Table XX).

TABLE XXXV—Continued

Planting Plan and Yields Obtained in that Part of the Nursery Used to Grow the Parents and the Minota-White Russian F₃ Families in 1921. Parents and Progeny Arranged in the Order in Which They Appeared in the Nursery

Culture number or parent	Open panicles						Side panicles					
	Resistant			Susceptible			Resistant			Susceptible		
	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield
		grams	grams		grams	grams		grams	grams		grams	grams
Minota												
4-4-31				41	48.3	1.18				11	13.9	1.26
4-4-32				32	47.1	1.47				10	13.4	1.34
4-4-33				27	35.8	1.33				8	7.7	0.96
4-4-34	24	46.5	1.94	21	35.5	1.69	9	18.7	2.08	3	6.0	2.00
4-4-35				7	12.1	1.73				1	2.4	2.40
Minota				38	61.5	1.62						
4-4-36	23	44.3	1.93	40	83.4	2.09	6	7.8	1.30	7	7.1	1.01
4-4-37				8	14.3	1.79				1	2.3	2.30
4-4-38				28	45.6	1.63				1	2.1	2.10
4-4-39	26	49.8	1.92				11	15.5	1.41			
4-4-40	28	51.2†	1.83	5	9.6	1.92						
Minota	28	57.6	2.06	36	67.7	1.88	9	13.0	1.44			
4-4-41	21	36.2†	1.72	5	9.8	1.96	7	13.5†	1.93	11	19.1	1.74
4-4-42	Eliminated											
4-4-43	Eliminated											
4-4-44	Eliminated											
4-4-45	Eliminated											
Minota	31	36.8	1.19	39	51.3	1.32				39	47.5	1.22
4-4-46				4	2.6	0.65				4	3.8	0.95
4-4-47	23	57.5	2.50	26	41.0	1.58	4	6.5	1.63	7	8.5	1.21
4-4-48				3	6.2	2.07						
4-4-49	25	48.8†	1.95	36	44.9	1.25						
4-4-50												
Minota	28	51.5	1.84	40	63.0	1.58	41	81.3	1.98	41	64.8	1.58
White Russian				9	15.4	1.71	25	33.2	1.33	12	12.3	1.03
4-4-51												
4-4-52	29	63.8	2.20	7	8.1	1.16						
4-4-53	26	36.8	1.42	15	18.8	1.25						
4-4-54												
4-4-55												
Minota	22	27.4	1.25	38	57.5	1.51	6	8.2	1.37	9	8.6	0.96
4-4-56	33	64.2	1.95	29	37.0	1.28	21	30.5	1.45	4	5.9	1.48
4-4-57				12	8.0	0.67						
4-4-58												
4-4-59												
4-4-60				8	10.2	1.28				8	10.8	1.35
										42	58.2	1.39

*Injured. †Corrected yield (See Table XX).

TABLE XXXV—*Continued*

PLANTING PLAN AND YIELDS OBTAINED IN THAT PART OF THE NURSERY USED TO GROW THE PARENTS AND THE MINOTA-WHITE RUSSIAN F_4 FAMILIES IN 1921. PARENTS AND PROGENY ARRANGED IN THE ORDER IN WHICH THEY APPEARED IN THE NURSERY

Culture number or parent	Open panicles — Resistant			Open panicles — Susceptible			Side panicles — Resistant			Side panicles — Susceptible		
	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield
		grams	grams		grams	grams		grams	grams		grams	grams
Minota												
4-4-61	20	38.5†	1.93	35	38.3	1.09	7	9.2†	1.31	7	11.1	1.59
4-4-62	Eliminated											
4-4-63	Eliminated											
4-4-64				27	39.1	1.45	31	63.6	2.05	11	16.2	1.47
4-4-65				42	54.8	1.30				40	53.5	1.34
Minota												
4-4-66	29	70.5†	2.43				10	20.1†	2.01			
4-4-67	17	39.0	2.29	4	7.4	1.85	6	15.5	2.58	3	8.3	2.77
4-4-68	29	79.4	2.74	9	14.1	1.57	10	19.7	1.97			
4-4-69	23	40.0	1.74	40	59.2	1.48	6	13.0	2.17	3	3.7	1.23
4-4-70				27	36.7	1.36				2	5.0	2.50
Minota	29	50.8	1.75				6	9.5	1.58	8	13.9	1.74
4-4-71												
4-4-72				6	8.0	1.33				2	1.6	0.80
4-4-73	Eliminated											
4-4-74	20	45.0	2.25				10	27.8	2.78			
4-4-75	25	78.9†	3.16	41	79.1	1.93	10	31.7†	3.17			
Minota												
4-4-76	26	62.1	2.39	8	16.5	2.06	27	61.8	2.29	13	29.6	2.28
4-4-77	35	76.3†	2.18				5	3.8	0.76	2	2.9	1.45
4-4-78												
4-4-79							38	73.9†	1.94			
4-4-80				35	55.2	1.58	29	43.4	1.50	11	16.2	1.47
Minota												
4-4-81	28	52.8†	1.89				7	10.8†	1.54			
4-4-82	24	40.1†	1.67				11	18.7†	1.70			
4-4-83	37	64.6	1.75									
4-4-84				10	7.5	0.75						
4-4-85	25	21.6	0.86	26	38.0	1.46				35	34.3	0.98
Minota												
4-4-86	31	61.5†	1.98									
4-4-87	31	87.9†	2.84									
4-4-88	26	50.4	1.94									
4-4-89				5	9.1	1.82	9	17.8	1.98	3	7.0	2.33
4-4-90				39	55.0	1.41	29	60.0	2.07	10	15.0	1.50

*Injured.   †Corrected yield (See Table XX).

TABLE XXXV—*Continued*

PLANTING PLAN AND YIELDS OBTAINED IN THAT PART OF THE NURSERY USED TO GROW THE PARENTS AND THE MINOTA-WHITE RUSSIAN F$_3$ FAMILIES IN 1921. PARENTS AND PROGENY ARRANGED IN THE ORDER IN WHICH THEY APPEARED IN THE NURSERY

Culture number or parent	Open panicles						Side panicles					
	Resistant			Susceptible			Resistant			Susceptible		
	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield
		grams	grams		grams	grams		grams	grams		grams	grams
Minota..........												
4-4-91..........	18	45.2	2.51	39	66.3	1.70	5	10.2	2.04	5	9.5	1.90
4-4-92..........				6	7.6	1.27	37	43.6†	1.18			
4-4-93..........				38	47.3	1.24						
4-4-94..........							20	50.8	2.54	5	6.3	1.26
4-4-95..........	27	58.3†	2.16				12	32.7†	2.73			
Minota..........												
4-4-96..........	30	62.6	2.09	38	77.8	2.05						
4-4-97..........	26	69.2	2.66	6	11.3	1.88	2	2.7	1.35	3	4.0	1.33
4-4-98..........				7	13.4	1.91	8	14.1	1.76	1	1.8	1.80
4-4-99..........	32	63.9†	2.00	32	56.1	1.75				10	17.2	1.72
4-4-100.........				39	83.5	2.14	29	57.8	1.99	8	12.8	1.60
Minota..........							41	92.1	2.25			
White Russian...												

*Injured.   †Corrected yield (See Table XX).

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TABLE XXXVI

PLANTING PLAN AND YIELDS OBTAINED IN THAT PART OF THE NURSERY USED TO GROW THE PARENTS AND THE VICTORY-WHITE RUSSIAN F_3 FAMILIES IN 1921. PARENTS AND PROGENY ARRANGED IN THE ORDER IN WHICH THEY APPEARED IN THE NURSERY

Culture number or parent	Open panicles — Resistant			Open panicles — Susceptible			Side panicles — Resistant			Side panicles — Susceptible		
	No. of plants	Total yield (grams)	Average yield (grams)	No. of plants	Total yield (grams)	Average yield (grams)	No. of plants	Total yield (grams)	Average yield (grams)	No. of plants	Total yield (grams)	Average yield (grams)
White Russian							41	92.1	2.25			
Victory	29	110.8*	3.82	31	37.6	1.21						
3-1-1				39	44.7	1.15						
3-1-2	5	4.2	0.84	7	7.6	1.09						
3-1-3							6	8.3	1.38	6	5.0	0.83
3-1-4							36	100.8*	2.80	6	6.5	1.08
3-1-5							23	50.3	2.19			
Victory												
3-1-6				26	24.3	0.93				5	4.5	0.90
3-1-7				28	25.0	0.89						
3-1-8	25	45.1	1.80	20	12.4	0.62						
3-1-9				7	6.0	0.86				42	51.7	1.23
3-1-10	25	62.6*	2.50				6	14.6*	2.43			
Victory				31	24.5	0.79						
3-1-11	19	33.2	1.75	5	8.0	1.60	9	14.3	1.59	3	6.0	2.00
3-1-12				23	36.5	1.59				12	24.2	2.02
3-1-13	23	60.2	2.62	7	11.3	1.61	5	7.5	1.50	5	10.1	2.02
3-1-14	25	45.1	1.80				4	9.5	2.38	2	2.0	1.00
3-1-15	24	39.0*	1.63	6	8.5	1.42	6	11.4*	1.90			
Victory				31	28.6	0.92						
3-1-16	21	48.0*	2.29				6	13.6*	2.27	37	40.6	1.10
3-1-17	16	21.8	1.36	3	1.8	0.60	5	8.0	1.60	3	2.0	0.67
3-1-18	19	45.2*	2.38				8	10.8*	1.35			
3-1-19										8	6.5	0.81
3-1-20												
Victory				23	28.5	1.24						
3-1-21	26	48.6	1.87	25	21.3	0.85						
3-1-22	27	53.3	1.97	6	6.8	1.13	6	10.4	1.73	2	3.2	1.60
3-1-23	19	30.0	1.58	5	6.2	1.24						
3-1-24				15	15.9	1.06						
3-1-25				36	26.1	0.73				8	16.8	2.10
Victory				15	18.3	1.22						
3-1-26				37	60.5	1.64				2	1.8	0.90
3-1-27				36	55.2	1.53				4	5.5	1.38
3-1-28	19	36.8	1.94	5	7.5	1.50	2	5.3	2.65	12	18.1	1.51
3-1-29	16	32.8	2.05	10	15.7	1.57	3	5.6	1.87	7	11.8	1.69
3-1-30				19	26.8	1.41	27	68.5	2.54			

*Corrected yields (see Table XX).

TABLE XXXVI—(Continued)

PLANTING PLAN AND YIELDS OBTAINED IN THAT PART OF THE NURSERY USED TO GROW THE PARENTS AND THE VICTORY-WHITE RUSSIAN F₃ FAMILIES IN 1921. PARENTS AND PROGENY ARRANGED IN THE ORDER IN WHICH THEY APPEARED IN THE NURSERY

	Open panicles						Side panicles					
	Resistant			Susceptible			Resistant			Susceptible		
Culture number or parent	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield
		grams	grams		grams	grams		grams	grams		grams	grams
Victory.												
3-1-31	22	61.6	2.80	44	50.2	1.14	4	12.8	3.20	3	4.5	1.50
3-1-32				6	7.1	1.18						
3-1-33	15	28.6	1.91	41	80.3	1.96						
3-1-34				17	13.2	0.78						
3-1-35				31	60.0	1.94				7	14.1	2.01
Victory.												
3-1-36	31	77.0	2.48	36	41.2	1.14						
3-1-37	30	64.3	2.14	28	32.4	1.16						
3-1-38				34	49.1	1.44	4	10.5	2.63	3	1.7	0.57
3-1-39				7	9.5	1.36				13	21.2	1.63
3-1-40	21	49.1	2.34	3	4.1	1.37	3	7.1	2.37	3	6.3	2.10
Victory.												
3-1-41	19	42.7	2.25	21	33.1	1.58	6	10.2	1.70	1	1.8	1.80
3-1-42	28	77.0*	2.75	8	9.3	1.16	2	6.0*	3.00			
3-1-43	22	43.6	1.98	40	29.5	0.74	5	14.4	2.88	1	1.5	1.50
3-1-44	24	49.6	2.07	6	8.3	1.38	6	12.1	2.02	2	3.7	1.85
3-1-45	14	30.9*	2.21	7	9.0	1.29	15	21.4*	1.43			
Victory.												
3-1-46	31	81.6*	2.63	4	7.8	1.95	29	63.1	2.18	11	20.9	1.90
3-1-47				29	36.6	1.26	4	7.8	1.95	3	7.4	2.47
3-1-48	12	29.8*	2.48	2	6.5	3.25						
3-1-49	29	84.3*	2.91	27	33.5	1.24				5	6.3	1.26
3-1-50				29	26.5	0.91						
Victory.												
White Russian.												
2-2-1	8	20.2	2.53	16	38.8	2.43	34	80.7	2.37	6	15.0	2.50
2-2-2	22	54.5	2.48	4	5.7	1.43	3	4.3	1.43	1	2.3	2.30
2-2-3	26	56.8	2.18	6	11.3	1.88	5	9.1	1.82	3	3.7	1.23
2-2-4	32	95.9*	3.00	7	15.4	2.20	4	7.8	1.95			
2-2-5	25	70.0	2.80	36	38.1	1.06	6	15.1	2.52			
Victory.												
2-2-6	27	64.3	2.38									
2-2-7	20	25.5*	1.28	10	7.7	0.77	7	8.9*	1.27	3	3.0	1.00
2-2-8	29	93.0*	3.21				5	10.0*	2.00			
2-2-9	25	59.8	2.39									
2-2-10				10	26.8	2.68				24	32.5	1.35

*Corrected yields (see Table XX).

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TABLE XXXVI—(Continued)

PLANTING, PLAN AND YIELDS OBTAINED IN THAT PART OF THE NURSERY USED TO GROW THE PARENTS AND THE VICTORY-WHITE RUSSIAN F₃ FAMILIES IN 1921. PARENTS AND PROGENY ARRANGED IN THE ORDER IN WHICH THEY APPEARED IN THE NURSERY

Culture number or parent	Open panicles						Side panicles					
	Resistant			Susceptible			Resistant			Susceptible		
	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield
		grams	grams		grams	grams		grams	grams		grams	grams
Victory	25	57.8	2.31	37	42.3	1.14	8	19.1	2.39	2	1.3	0.65
2-2-11				5	8.0	1.60				8	9.1	1.14
2-2-12				26	30.5	1.17						
2-2-13							26	45.5*	1.75			
2-2-14	3	3.5	1.17	26	17.1	0.66	2	3.2	1.60	7	8.7	1.24
2-2-15							24	57.8	2.41			
Victory	22	45.3	2.06									
2-2-16				30	23.4	0.78				4	2.3	0.58
2-2-17				20	23.2	1.16				36	27.7	0.77
2-2-18										41	56.7	1.38
2-2-19				9	10.1	1.12	2	3.3	1.65	4	4.5	1.13
2-2-20							23	34.6	1.50	9	7.8	0.87
Victory	22	50.0	2.27	40	50.8	1.27						
2-2-21	23	52.8	2.30	7	9.2	1.31	5	9.5	1.90	4	2.5	0.63
2-2-22	27	46.2	1.71	7	15.3	2.19	5	6.5	1.30	4	3.6	0.90
2-2-23	23	35.3	1.53	6	2.0	0.33	4	9.7	2.43	2	2.3	1.15
2-2-24	20	37.4*	1.87	6	5.7	0.95						
2-2-25							5	6.2*	1.24			
Victory	21	26.6	1.27	33	27.6	0.84						
2-2-26				10	4.8	0.48				6	7.8	1.30
2-2-27				26	41.1	1.58				6	5.3	0.88
2-2-28							30	46.3	1.54	41	44.4	1.08
2-2-29										36	46.3	1.29
2-2-30												
Victory	20	34.8	1.74	44	36.8	0.84						
2-2-31	24	41.7*	1.74	11	12.9	1.17	2	2.5	1.25	4	7.8	1.95
2-2-32							5	10.0*	2.00			
2-2-33				33	32.5	0.98						
2-2-34	29	52.8*	1.82				29	44.7*	1.54			
2-2-35												
Victory	20	29.5	1.48	31	26.8	0.86	6	17.4	2.90			
2-2-36	18	27.1*	1.51	6	7.1	1.18				3	3.6	1.20
2-2-37	19	32.6	1.72									
2-2-38	21	31.0	1.48	6	10.1	1.68	10	16.0	1.60	2	1.8	0.90
2-2-39	21	33.5	1.60	5	8.2	1.64	3	3.5	1.17	4	2.0	0.50
2-2-40							6	8.6	1.43			

*Corrected yields (see Table XX).

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TABLE XXXVI—(Continued)

PLANTING PLAN AND YIELDS OBTAINED IN THAT PART OF THE NURSERY USED TO GROW THE PARENTS AND THE VICTORY-WHITE RUSSIAN F₃ FAMILIES IN 1921. PARENTS AND PROGENY ARRANGED IN THE ORDER IN WHICH THEY APPEARED IN THE NURSERY

Culture number or parent	Open panicles — Resistant			Open panicles — Susceptible			Side panicles — Resistant			Side panicles — Susceptible		
	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield	No. of plants	Total yield	Average yield
		grams	grams		grams	grams		grams	grams		grams	grams
Victory........												
2-2-41	18	44.1	2.45	37	44.8	1.21	5	15.1	3.02			
2-2-42	11	33.6	3.05	5	3.4	0.68	2	2.8	1.40	2	1.5	0.75
2-2-43				16	37.6	2.35				10	20.3	2.03
2-2-44	15	32.4	2.16	7	10.6	1.51	2	2.8	1.40	4	8.4	2.10
2-2-45	20	41.3	2.07	9	14.3	1.59				2	3.0	1.50
Victory........				7	12.1	1.73						
2-2-46	19	37.2	1.96	36	39.1	1.09	10	13.8	1.38			
2-2-47	21	39.1	1.86	6	5.5	0.92	4	11.3	2.83	1	2.0	2.00
2-2-48	Eliminated			5	5.5	1.10						
2-2-49	17	42.5	2.50	6	6.3	1.05	9	19.8	2.20	4	6.5	1.63
2-2-50												
Victory........												
White Russian..				34	38.0	1.12	36	71.1	1.98	39	49.3	1.26

*Corrected yields (see Table XX).

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The   University   of   Minnesota
Agricultural Experiment Station

The Determination of Biologic Forms
of Puccinia Graminis on Triticum Spp.

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The University of Minnesota
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Department of Agriculture*

THE DETERMINATION OF BIOLOGIC FORMS OF PUCCINIA GRAMINIS ON TRITICUM SPP. [1]

By E. C. Stakman and M. N. Levine

It has been shown (1, 2, 3, 4)[2] that *Puccinia graminis tritici* (Pers.) Erikss. and Henn. in reality consists of several biologic forms which can be recognized by their action on different varieties of wheat (*Triticum vulgare, T. durum, T. compactum*), Emmer (*T. dicoccum*) and Einkorn (*T. monococcum*). Stakman, Levine and Leach (3) stated that they had found about a dozen such forms. Thirty-seven are now known and a method has been developed for their identification.

Since there have been a considerable number of inquiries regarding the methods used, and since the complete results cannot be published for some time, it seems desirable to publish, in advance of a more detailed presentation of the results, a description of the methods employed and a summary of the behavior of the biologic forms discovered.

All of the known forms can be identified by their parasitic action on the twelve "differential hosts" which are listed in Table I. These varieties of *Triticum spp.* were selected from a much greater number which were originally used. It is likely that many more forms could be recognized if the proper combination of differential hosts were employed.

TABLE I

List of Differential Hosts Used in Identifying Biologic Forms of Stem Rust of Wheat

Triticum compactum
    Little Club, C. I.* No. 4066
Triticum vulgare
    Marquis, C. I. No. 3641 (Minn. 1239)
    Kanred, C. I. No. 5146 (Kans. 2401)
    Kota, C. I. No. 5878 (N.D. 10003)
Triticum durum
    Arnautka, C. I. No. 4072 (S.D. 150)
    Mindum, C. I. No. 5296 (Minn. 470)
    Arnautka (Speltz Marz), C. I. No. 6236 (Minn. 337)
    Kubanka, C. I. No. 2094
    Acme, C. I. No. 5284 (S.D. 284)
Triticum monococcum
    Einkorn, C. I. No. 2433
Triticum dicoccum
    White Spring Emmer, C. I. No. 3686 (Minn. 1165)
    Khapli, C. I. No. 4013

* C. I.=Cereal Investigations accession number.

[1] Coöperative investigations between the Agricultural Experiment Station of the University of Minnesota and the Bureau of Plant Industry of the United States Department of Agriculture.

[2] Reference is made by number to literature citations.
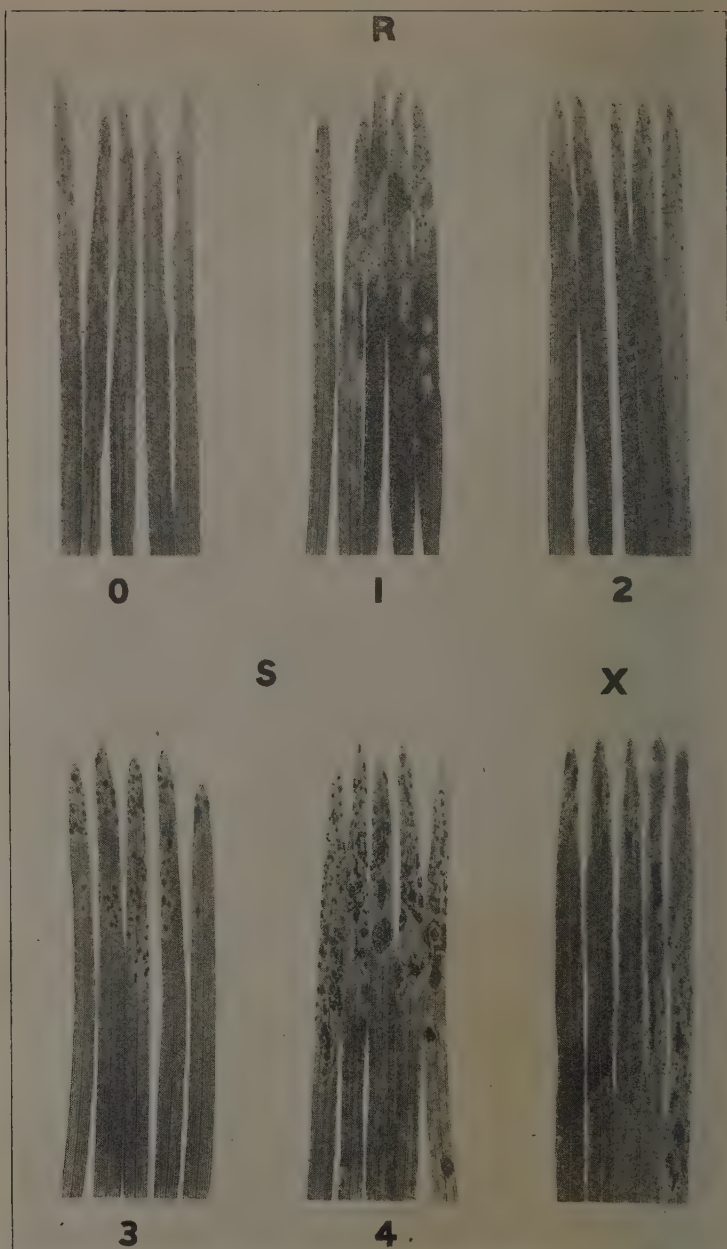
Fig. 1. Different types of infection produced by biologic forms of *Puccinia graminis* on various differential hosts of *Triticum spp.* Class R, indicating resistance, includes types 0, 1 and 2; class S, designating susceptibility, includes types 3 and 4; class X, representing the heterogeneous type of infection, has no subdivisions.

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The varieties listed in Table I are inoculated in the usual manner and incubated for 48 hours. While single-spore isolations should be made for very careful work, it is not necessary for the purpose of a general survey. Whenever possible all of the differential hosts should be inoculated at the same time and kept under the same environmental conditions subsequently. The best results will be obtained by keeping the inoculated plants under optimum conditions for the normal development of the rust. An abundant supply of sunlight is highly essential.

The types or classes of infection are indicated by arabic numerals from 0 to 4 in order of severity of infection, 0 indicating practical immunity and 4 complete susceptibility. Fluctuations within a class have been designated by plus and minus signs. In addition to the five types above mentioned, there is a sixth type which is represented by x. On the same plant various degrees of infection may occur, apparently ranging from 1 to 4. It has been shown that this is quite characteristic of the action of some biologic forms on certain varieties and it should be distinguished clearly from mixed infections due to the presence of two or more biologic forms on the same plant. The various types of infection will be clear from Plate I and Table II. Cross inoculations are sometimes necessary before a final determination can be made.

TABLE II

EXPLANATION OF SYMBOLS USED TO INDICATE TYPES AND DEGREES OF INFECTION PRODUCED BY BIOLOGIC FORMS OF PUCCINIA GRAMINIS ON VARIETIES OF WHEAT

Types of Infection

0 — IMMUNE

No uredinia developed; hypersensitive flecks usually present, but sometimes there is apparent absolutely no trace of mycelial invasion in the host tissues

1 — VERY RESISTANT

Uredinia minute and isolated; surrounded by sharp, contniuous, hypersensitive, necrotic areas

2 — MODERATELY RESISTANT

Uredinia isolated and small to medium in size; hypersensitive areas present in the form of necrotic halos or circles; pustules often in green, but slightly chlorotic, islands

3 — MODERATELY SUSCEPTIBLE

Uredinia medium in size; coalescence infrequent; development of rust somewhat subnormal; true hypersensitiveness absent; chlorotic areas, however, may be present

4 — VERY SUSCEPTIBLE

Uredinia large, numerous and confluent; true hypersensitiveness entirely absent, but chlorosis may be present when cultural conditions are unfavorable

x — HETEROGENEOUS

Uredenia very variable, apparently including all types and degrees of infection on the same blade; no mechanical separation possible; on reinoculation small uredinia may produce large ones, and vice versa. Infection ill defined

Degrees of Infection

(=) — TRACE

Uredinia very few in number and covering a limited surface; development of rust generally poor and decidedly subnormal

(–) SLIGHT

Rust development below normal, but somewhat better than "trace"

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(±) — MODERATE

Variation in rust development from "slight" to "considerable"; when infection is uniform but only medium in quantity the symbol is omitted

(+) — CONSIDERABLE

Infection better than normal; uredinia fairly numerous and scattered

(++) — ABUNDANT

Luxuriant development of rust; uredinia very many, covering large area of affected host

Miscellaneous Symbols

(;) — Hypersensitive flecks
(.) — Necrotic lesions

After the type and degree of infection on the differential hosts have been recorded, it is relatively easy to determine the biologic form by the use of the dichotomous key given in Table III. Plants on which the degree of attack is from 0 to 2 are considered resistant and those on which the degree is 3 or 4 are considered susceptible. Those on which the heterogeneous type of infection develops are, of course, in the x class. In the key only these major differences are recognized. The actual determination of biologic forms, therefore, is made by determining only whether the differential hosts are susceptible or resistant or whether they react in the peculiar manner designated by x.

TABLE III

Analytical Key to Biologic Forms of Puccinia Graminis Within the Genus Triticum

```
Infection homogeneous on all differential hosts
    Marquis resistant (R)
        Kanred resistant
            Kota resistant
                Arnautka resistant
                        Kubanka resistant ...........................................II
                        Kubanka susceptible
                                Einkorn resistant ........................XXVII
                                Einkorn susceptible ........................XXIII
                    Arnautka susceptible
                        Mindum resistant .....................................VI
                        Mindum susceptible
                                Kubanka resistant .............................IV
                                Kubanka susceptible
                                        Einkorn resistant ......................XVI
                                        Einkorn susceptible ....................XIV
                Kota susceptible
                        Mindum resistant .....................................XXVIII
                        Mindum susceptible .....................................XIX
            Kanred susceptible
                Arnautka resistant
                        Kubanka resistant ........................................VII
                        Kubanka susceptible ....................................XXXIII
                Arnautka susceptible ...............................................X
    Marquis susceptible (S)
        Kanred resistant
                Kota resistant ...............................................XXIV
                Kota susceptible
                        Arnautka resistant ...........................................I
                    Arnautka susceptible
                                Mindum resistant ...............................XXVI
                            Mindum susceptible
                                Kubanka resistant
                                        Emmer resistant ..........................V
                                        Emmer susceptible ......................VIII
```

6

The use of the key is very simple. For instance, Marquis is either resistant or susceptible. Assuming it is susceptible it then is necessary to know how Kanred reacts. If Kanred is resistant and Arnautka is also, then it is Form 1; but if Arnautka is susceptible, then the reaction of Mindum must be known, etc. It will be noted that neither Little Club nor Khapli appears in the key. This is because Little Club is susceptible to all known forms and Khapli is highly resistant to all of them.

When the form has been run down by the key, it is necessary to check up with the known action of each form as indicated in Table IV. If the infection capabilities agree with those indicated for the form, the identification is complete; if they do not, then either the form is undescribed or there may be a mixture of forms and it becomes necessary to separate them.

TABLE IV

Variations and Constants in Reaction of Differential Hosts of Wheat to Biologic Forms of Stem Rust

Ranges and means of infection

Biologic form	Little Club Range	Little Club Mean	Marquis Range	Marquis Mean	Kanred Range	Kanred Mean	Kota Range	Kota Mean	Arnautka Range	Arnautka Mean	Mindum Range	Mindum Mean	Sht. Mars Range	Sht. Mars Mean	Kubanka Range	Kubanka Mean	Acme Range	Acme Mean	Einkorn Range	Einkorn Mean	Emmer Range	Emmer Mean	Khapli Range	Khapli Mean
I	3+ 4+	4	3+ 4+	4	0	0	3-	3+	0. 1	1=	0 2+	1	0. 1+	1=	3- 4	3+	3 4	3+	3- 3+	3	0 1	0;	0 1+	1=
II	4- 4+	4	1= 2+	2=	0 2+	0;	0 2	2=	0 1+	1-	0 2+	1	0 1+	1=	0 2	1+	3- 4+	3+	3- 4	3+	0; 1	1-	0 1	0;
III	3+ 4+	4	3+ 4+	4	4+	4	4 4	3+	0 2-	1=	0 2+	2+	0 2+	1-	0 2	1+	4 4+	3+	3- 4	3+	0 2-	1=	0 1+	0;
IV	4	4	2+ 4	2+	2+	2+	2	4	3+ 4	4	3 4	3+	3 4	3+	0; 2+	2	3 4	3+	3- 4	3+	0. 1+	1=	0 1+	1=
V	3+ 4+	4	4 4	4	0	0	3+ 4	3	3 4	4	3 4	3+	3- 4	3+	0; 2+	1+	3- 4	3+	3 4	3	0 1-	0;	0	0;
VI	4	4	0; 2+	2	0	0	0 1	0;	0. 1	3+	0; 2-	2-	0 2	2=	0 2	1	3 4	3+	3 4	3	0 0.	0.	0 1	0;
VII	3+ 4+	4	0	4	0 1-	1=	0 1+	1=	0. 1	1=	0 1+	1+	0 2	1-	0 2	1	3 4	3+	3- 4	3-	0 2	1	0 1+	1-
VIII	3+ 4+	4	3+ 4+	4	0;	0;	3= 4	4	3- 4+	4	3 4	3+	3- 4+	4	0; 2-	0.	3- 4	3+	3- 4	3	3+ 4	4	0; 1-	0;
IX	3+ 4+	4	4 4	4	4	0;	3= 4	3+	3+ 4+	4	3- 4	4	3- 4+	4	3- 4	4	3- 4	4	3- 4	3+	3- 4	4	0	1=
X	3+ 4+	3+	3+ 4+	3+	3+ 4	0.	1= 4	3+	3+ 4-	4	3- 4	4	3 4+	4	0; 3-	4	3- 4	4	3 4	3+	3- 4	1=	0; 1-	1=
XI	3 4	4	3+ 4	4	3+ 4	4	3= 4	2	3= 4	3+	0. 2-	1	0. 2+	1+	0; 2+	1+	3- 4	3+	3- 4	3	0 1	1=	0 1	1=
XII	3+ 4+	4	4 4	4	4	3+	4 4	3+	3+ 4	4	3- 4+	3+	0. 4	3+	1 4	3+	3- 4+	3+	3- 4	3+	0; 2	1=	0 1-	1=
XIII	3- 4+	4	4 4	4	3 4	3+	3= 4	3+	3- 4	3+	3 4	3+	3 4	3+	3 4	2-	3- 4	3+	3- 4-	3	0. 1+	1	0 1-	0;
XIV	3- 4+	4	1= 2+	2+	2+	1-	2+ 4	1+	3- 4	3+	3+ 4	3+	3 4	3+	3- 4	3+	3+ 4	3+	3- 4	3+	0; 2	1=	0 1+	1=
XV	3+ 4+	4	4+ 4	4	4	4=	4 4	3+	3- 4	4	4 4	4	3- 4+	4	3- 4	3+	3- 4	3+	3- 4	4	3 4	4=	0 4	1=
XVI	3- 4+	4	2	2=	0	0	1= 1+	1	3- 4	3+	3= 4	3+	3 4	3+	3+ 4	3+	3+ 4	4=	0	1-	0; 1-	1=	0; 1+	1

XVII....
XVIII...
XIX.....
XX......
XXI.....
XXII....
XXIII...
XXIV....
XXV.....
XXVI....
XXVII...
XXVIII..
XXIX....
XXX.....
XXXI....
XXXII...
XXXIII..
XXXIV...
XXXV....
XXXVI...
XXXVII..

It is not always possible to distinguish easily between infections due to a mixture of forms and that infection caused by forms producing an x reaction on certain varieties. Cross inoculations and inoculations made from the different types of uredinia only can be relied upon in such cases.

The methods described can naturally be modified to meet the requirements of individual investigators, but it seems likely that preliminary indications at least can be obtained by the use of the differential hosts listed in Table 1.

A complete summary of the results to date will be published later.

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The University of Minnesota
Agricultural Experiment Station

Sale Prices as a Basis for Farm Land Appraisal

By G. C. Haas
Division of Agricultural Economics

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UNIVERSITY FARM, ST. PAUL

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SALE PRICES AS A BASIS FOR FARM LAND APPRAISAL

By G. C. Haas*

The analysis of land valuation ordinarily resolves itself into four phases, as follows: (1) the general structure of land values; (2) geographical variations in land prices, as between states and sections of the country; (3) movements in land prices; (4) local variations in land prices. This study is confined to the fourth phase, local variations. The method of analysis has been to correlate the sale prices of 160 farms in Blue Earth County, Minnesota, sold in 1916, 1917, 1918, and 1919, with the factors influencing land prices, namely, value of buildings per acre, type of land, crop yields, distance from market, size of adjacent city or village, and type of road upon which located, and to derive from this correlation an equation from which the probable sale price of any other farm land in the same general territory may be determined.

This method assumes that land sale prices are the best basis for an appraisal policy. Appraising land means forecasting or predicting what it would sell for on the basis of the present market. The figure sought is probable market price, and not what any person, no matter how good his judgment, thinks the land should be worth. Market prices are the results of the judgments of the land market composed of buyers and sellers of the general order of intelligence.

Many persons consciously or unconsciously assume that the only scientific basis for land appraisal is the productivity of the land. While it is true that land derives its value solely from its products, and, therefore, its value must be proportional to the value of its product, nevertheless its productivity can not be made the basis for its appraisal, for several reasons, as follows: (1) The product of land is perpetual and no one can forecast the amount or value of it or determine the present worth of future products. To determine the present worth, one must know the rate at which land income is capitalized now and in the future. (2) The product required is net product, and to obtain net product, one must have costs of production. Several of the important costs of production, such as value of family labor and wages of management and responsibility-taking, can not even be estimated. There is a very wide range in net product on different farms if the profits of farmers are included in net product. Also many costs of production, such as taxes, fertilizers, wages, are likely to be different in the future. (3) It is impossible to determine the income from farm

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land from its use as residence and all the elements of psychic income associated with this. For all these reasons, no reputable scientific method of appraisal can be based on productivity.[1]

The land market.—Since the sale prices we are analyzing are actual market prices, we must consider the nature of the market in which these prices are made. The concept of a market needed for this purpose must be carefully drawn. Following are several statements concerning a market which are significant in this connection: "A market * * * is the totality constituted by a group of competing sellers over against a group of competing buyers concerned in exchanging the same commodity."[2] "Economists understand by the term market, not any particular market place in which things are bought and sold, but the whole of any region in which buyers and sellers are in such free intercourse with one another that the prices of the same goods tend to equality easily and quickly."[3] "Originally a market was a public place in a town where provisions and other objects were exposed for sale, but the word has been generalized so as to mean any body of persons who are in intimate business relations and carry on extensive transactions in any commodity. * * *. The traders may be spread over a whole town, or region of country, and yet make a market, if they are, by means of fairs, meetings, published lists, the post-office or otherwise, in close communication with each other."[4]

The essential idea of a market is organization. The organization is usually informal and unconscious, but it may become conscious and formal. This organization furnishes contacts or means of communication between the buyers and sellers in the market. A market is "perfect" or "ideal" to the extent that the organization is complete and all persons in it are constantly and instantly in full knowledge of one another's offers and acceptances. In a perfect market, either the commodity sold is uniform or else there is complete and accurate knowledge of all differences in it. Obviously, in such a market there can be but one price for the same thing at the same time.

The land market is certainly not a perfect market. Wherein does it fail? First of all, the commodity bought and sold is not uniform. This would make no difference, however, if the elements of variation in it were perfectly comprehended. But this we know to be far from the case. Determining the extent to which the elements of difference in land are actually reflected in differences in prices, in spite of the

[1] See Bulletin of the International Institute of Agriculture, Nos. 10-12, October-December, 1912, "The Value of Landed Property" by Frederick Aereboe, Chief of the Division of Rural Economy at the Royal School of Agriculture, Berlin. "The so-called valuation according to revenue is impracticable, unscientific and indefensible." p. 2343.

[2] Taylor, F. M., "Principles of Economics," p. 210. 5th ed.

[3] Cournot. "Recherches sur les Principes Mathématiques de la Théorie des Richesses."

[4] Jevons. "Theory of Political Economy." Ch. III.

imperfections of the land market, is of course a major problem of this investigation. The local variations or elements of difference in land will be analyzed a little later. Second, the land market is not well organized. There is no extensive or efficient means of disseminating information among buyers and sellers. There may be comparatively few buyers and sellers competing at any one sale. All sellers are not able to put their offerings before all the purchasers and also all buyers do not have a chance to provide all sellers with an opportunity to sell to them.

Because they lack bargaining power, or are at an economic disadvantage, buyers and sellers are not always able to act rationally on information received. Also, many buyers and sellers are frequently influenced by non-economic motives, such as home ties, caprice, passion, and prejudice. Professional land salesmen have more than average knowledge concerning the land market and usually have the advantage when it comes to bargaining, and, of course, succeed in making many sales of the same grade of land at different prices.

In spite of all these circumstances, however, the general tendency on the part of both buyers and sellers is to investigate the market rather thoroly, the buyers seeking for the best bargain, and the sellers seeking for the purchaser offering the high price. The mere fact that those who do not deal cautiously and with discretion are known in the land market as "suckers," and the sales resulting as "sucker sales," indicates that such sales are not common. The land market surely tends to operate in such a way as to cause the same grade of land to sell in the same market at the same time at like prices, altho the adjustment is never perfect and there is always some variation in the market price of the same grade of land. Such variation as there may be is, of course, of much importance in the operation of a system which aims to predict the market price of land on the basis of sale prices. The results of this investigation will throw some light on the importance of this variation.

  The basis of land values.—To explain the significance of local differences in land, we must understand the basis of land values. Land has value because it produces an income in the form of materials or services that satisfy human wants. The income may be material or psychic or both. The material income appears in the products of the soil, the psychic income in wants directly satisfied by it, such as the want for a site for a home in a good neighborhood on a good road near a city or village.

Land yields these incomes in perpetuity. The value of a piece of land is the present worth of its incomes in perpetuity. If it can be assumed that the future incomes will all be the same as present incomes, then the value of land is expressed by the formula:

$$V = \frac{a}{r}$$

when V = the value of the land, a = its annual net income, and r = the prevailing rate of interest.[5] This, of course, is simply the formula for deriving the value of a constant-income bearer by capitalizing the income.

It is not reasonable to assume, however, that the future incomes from land will be the same as the present incomes. It is usually assumed that because of increase in population, future incomes will be greater than present incomes. The formula for capitalizing an income increasing at a constant arithmetical rate is as follows:

$$V = \frac{a}{r} + \frac{i}{r^2}$$

where i = the increase in income. In applying this to land, however, one must realize that we do not know what the increases in incomes will be. Hence i must represent "anticipated increase in annual income." Let us assume, for example, that for a given farm, the value of a per acre is $5, that r is 5 per cent, and that a is expected to increase at the rate of 10 cents per year. Substituting in the formula:

$$V = \frac{5.00}{.05} + \frac{.10}{(.05)^2} = 100 + 40 = 140$$

The value of this land per acre is $140, of which $40 is based on anticipated increase in income.

The prevailing opinion as to future incomes, therefore, plays a large role in determining land values. Land values never represent present earning power capitalized. Different farmers and real estate men have greatly varying ideas as to the future of land incomes. However, to the extent that the land market is a perfect market, one level of opinion as to future income becomes the market level, and those who have a less optimistic idea of the future either do not buy or sell too cheaply, or perhaps sell for more than they think their land is worth. In any one county, such as Blue Earth County, in normal times this market level of opinion is likely to be fairly well established. The future element in land values, therefore, is not so serious a complication in a study of local variations as one would at first think.

    [5] Fisher. "The Nature of Capital and Income." p. 202. Taylor. "Agricultural Economics." p. 206.

It can be said safely that in no case does the buyer or seller of a farm have the exact income data before him. He may know with a fair degree of accuracy what the physical income of the land is for one year, or past years, but he does not know it for the future. He will have only a fairly definite idea of what the psychic income is worth to him. But buyers and sellers do not attack the problem in this way. Instead, they proceed by comparison and analogy. They compare the farm in question with other farms with the incomes or values of which they are familiar. All factors in the farm in question which may influence income are compared with known cases where they can approximate their effect. Any farm, therefore, becomes to them a combination of factors which affect income or value.

The method of attack in this investigation is essentially that of the prospective buyer.

To analyze market prices successfully, one must follow up the channels of thought of those who make the market prices. A good appraisal system for land should analyze as the market thinks. Practical men will go further and say that the only method by which land can be appraised is to call in several men of good sense and judgment and let them analyze in the manner of prospective buyers; in other words, make "an experienced guess." Such men are given to saying that "every farm is a thing by itself," and that therefore it is impossible to combine a large number of farms in one analysis and obtain any results worth while. Modern statistical science, however, does offer a workable method of doing this. If accurate measures of the factors influencing land values can be obtained, it is entirely possible by tabulation and partial and multiple correlation methods to determine the weights or significance of the various factors. These are the methods used in this investigation. They are described in detail later.

In every territory the factors which influence value are somewhat different. In the section studied, the following factors were considered: (1) The 1919 depreciated cost of buildings per acre; (2) land classification, or the amounts of the different types of land; (3) productivity of the soil, represented by relative crop yields; (4) distance to market; (5) type of road; (6) size of market town. These factors will be explained later in detail.

THE AREA

Blue Earth County was selected as an area in which to work out the problem because it is more than usually uniform as to soil, topography, and systems of farming, and because at the same time it offers the necessary variations in village and city centers, types of roads, and the like. It was thought best not to complicate the problem too much

at the start by choosing too heterogeneous an area; if the method attained promising results in a simple area, after being further developed it could be applied to a more difficult one. Furthermore, Blue Earth County is one of the few counties in Minnesota for which there is a soil survey.

Blue Earth County is in south central Minnesota, on the south side of the Minnesota river, not far from the city of Mankato, where the river bends northward. Figure 1 shows the Blue Earth river with its tributaries, the Le Sueur, the Maple, the Big Cobb and Little Cobb rivers, converging within a radius of ten miles from the confluence of the Blue Earth with the Minnesota river at Mankato. The area is a flat gently rolling expanse with an imperceptible slope from east, south, and west toward Mankato. "The country in the neighborhood of streams, where erosion has been most active, is always
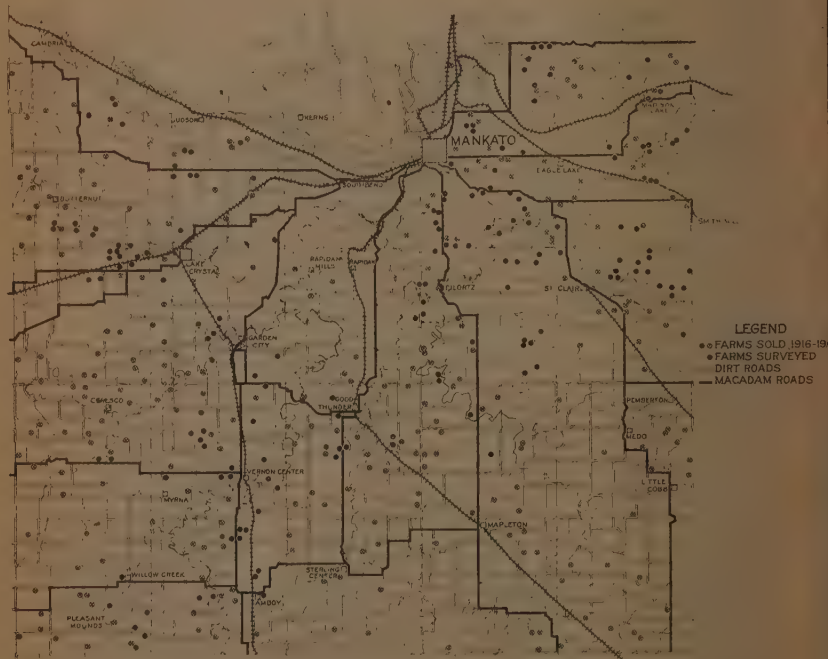
Fig. 1.   Location of Farms Covered in the Survey

more or less broken and rolling. Some of this is too rough for profitable cultivation. The land surface is interrupted here and there by glacial lakes varying in size from those too small to be represented on a map to bodies of two square miles in extent. The principal lakes in order of size are Jackson, Madison, Eagle, and Loon. About five-sixths of the area was originally prairie. The streams and lakes were fringed with a narrow strip of timber."[6]

The land area of the county is 749 square miles, or 479,104 acres. Table I gives the census information as to the agriculture of the county. The system of farming prevailing is a modification of the corn, cattle, and hog farming of the Corn Belt. More wheat is grown than in the Corn Belt, and it is mostly spring wheat in place of winter wheat. Also more hay and forage are grown, and the cattle industry includes nearly as much dairying as beef in many sections of the country. Hog-raising is important, but of course not so important as in the Corn Belt. Exclusive stock and dairy farms are few in number, but the increase in dairying has been rapid in recent years. Sheep-raising is practiced

[6] Soil Survey of Blue Earth County, Minnesota, pp. 873-5.

SOIL MAP
OF
BLUE EARTH COUNTY
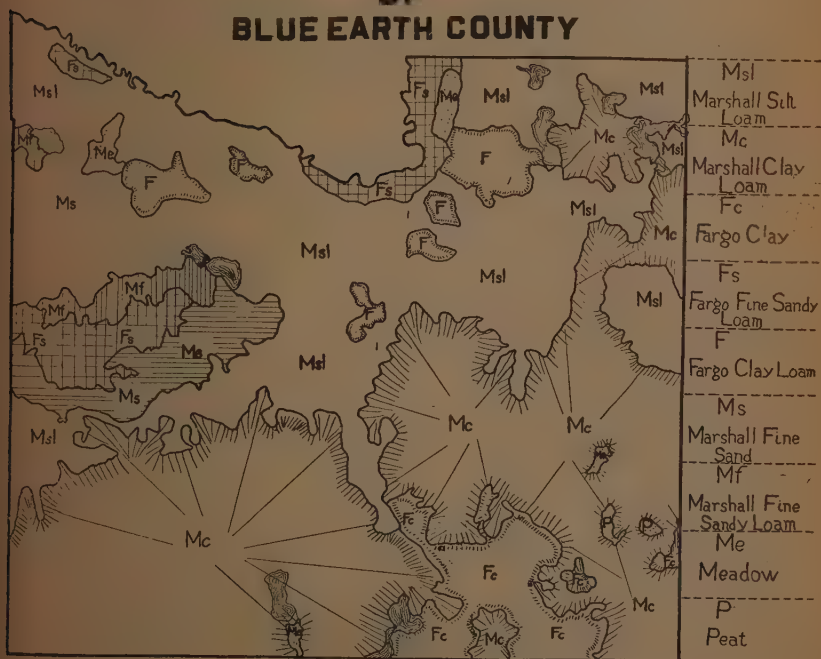
Fig. 2. Distribution of Soil Types

especially on farms which are adapted to grasses or are infested with quack grass. The principal crops raised in order of acreage are hay, corn, wheat, oats, barley, and rye.

Soils.—All but 8.4 per cent of the soils of Blue Earth County belong to two soil series, namely, the Marshall and Fargo series; and 79.2 per cent belong to the Marshall series alone. The Marshall soils, predominating in the uplands, are the typical dark-colored glacial-till soils with high organic content occurring throughout the Corn Belt. The Fargo soils, predominating in the flat areas and depressions, are the black sticky soils that occur in the Red River Valley.

By soil types, 85.4 per cent of the soil is classed as loam, 5.8 per cent as clay, 4.0 per cent as meadow, 3.3 per cent as fine sand, 1.6 per cent as peat, and 0.6 per cent as sand. Of the loams, 43.7 per cent are clay loams, 29.7 per cent are silt loams, and 7.5 per cent are fine sandy loams. All these loams are first-class soils, except perhaps for the Fargo fine sandy loam (1.6 per cent) which is only fair. Altogether, aside from the meadow and peat areas, only about 7 per cent of the soil is not of good quality. Much of it is, however, quite heavy and can not be worked when it is wet, but it holds moisture well and produces large yields. Some of it, to be sure, has to be tiled to make it good farming land.

Figure 2 shows the general distribution of the principal soil types. Many small areas of peat and meadow are, of course, not shown; likewise many small included areas of soils of other types. The Marshall loam is included with the Marshall silt loam; also the Mankato sand with the Fargo fine sandy loam. Also the narrow fringes of Wabash soils along the rivers are included with the adjoining soils.

The 160 farms used in the survey are located on soil types as follows:

Marshall silt loam... 42
Marshall clay loam... 41
Fargo clay loam... 13
Marshall clay loam and Fargo clay loam..................... 23
Marshall silt loam and Marshall clay loam.................. 19
Marshall loam 3
Wabash fine sandy loam and Marshall silt loam............. 6
Marshall fine sand and Marshall fine sandy loam........... 5
Other combinations 8

Thus 61 of the 160 farms have two or more soil types indicated on the soil map. This does not include areas of peat and meadow found on a large number of the farms, and areas of other soils too small to be shown on the map.

TABLE I
BLUE EARTH COUNTY AGRICULTURAL STATISTICS, 1920 CENSUS

Number of farms..	2,954
Per cent of land area in farms...	90.3
Per cent of farm land improved..	80.7
Average acreage per farm..	149.1
Average improved acreage per farm..	120.3
Per cent of farms operated by owners......................................	68.6
Per cent of farms operated by tenants.....................................	30.8

Livestock

	Total No.
Horses	17,476
Beef cattle...	19,365
Dairy cattle..	32,470
Sheep	7,319
Swine	61,318

Crop Acreage	Acres
Corn	70,325
Oats	42,265
Wheat	66,227
Barley	3,820
Rye	3,462
Hay and Forage..	76,625

Markets.—Mankato, the county seat, with a population of 12,469 in 1919, is an important railroad and manufacturing center. The only other important towns are Lake Crystal, Vernon Center, Garden City, Amboy, Mapleton, Good Thunder, Madison Lake, and Eagle Lake, with populations ranging from 300 to 1200. The transportation and market facilities are good. Only a small proportion of the county is situated more than ten miles from a shipping point. The county is served by four railway lines; the Chicago Great Western; the Chicago, St. Paul, Minneapolis & Omaha; the Chicago, Milwaukee & St. Paul; and the Chicago & Northwestern. There are grain elevators and stockyards at convenient points along these lines everywhere throughout the county; also flour mills at various towns with outputs of from 50 to 1000 barrels a day. Keen railroad competition makes freight rates moderate and provides rapid service to Omaha, Minneapolis, St. Paul, Chicago, and other large cities. Thus there are ready outlets for any kind of produce.

Population.—The population of the county in 1919 was 31,477, made up of Americans, Germans, Swedes, Norwegians, and Welsh, named in order of relative numbers. The Welsh are in the Lake Crystal neighborhood, and the Germans in the section southwest of Vernon Center. The population is cosmopolitan everywhere, however; it is not uncommon to hear several languages spoken in one small community. As a rule, the farmers are hard-working and prosperous. Many of the farmers have acquired considerable wealth and now live in towns and rent their farms. In general the farm houses are neat and substantial.

METHOD OF SECURING DATA

The farms which were considered were those which were actually sold during the four-year period, 1916 to 1919 inclusive. The sale prices which were used are the considerations which were given when the transfer of deed was recorded, as collected by the Minnesota State Tax Commission.[7] In compiling these records, the Tax Commission discards all sales considerations which do not seem to be bona fide, such as those arising from trades, from transfers to relatives, and the like. The Tax Commission finally submits the reports on each farm to real estate men and bankers in each community, and these men weed out any which appear fictitious to them. As a result, the sale prices used in the study represent bona fide sales as nearly as it is possible to obtain them.[8]

The following information for each farm was transferred to cards before the field work was started. Also a map was prepared showing the location of the farms to be included. Each farm was marked with a number.

Date of Sale, March 1, 1919.   Number———

Seller, A. Churchyard.   Buyer, W. J. Cornhill

Legal description, $S\frac{1}{2}$ of $N\frac{1}{2}$ of $SW\frac{1}{4}$ and $W\frac{1}{2}$ of $S\frac{1}{2}$ of $SW\frac{1}{4}$

Section 32, township 108, range 20, 80 acres.

Consideration, $12,400

Assessed value of land, $8,160

Assessed value of buildings, $1,000

Assessed value of farm, $9,160

Appendix A presents a copy of the schedule used in the field together with the instructions for its use. The purchase price of the farm appears only on the card.

Very little difficulty was experienced in taking the records. The dimensions of buildings were actually measured in most cases. The farmers did not always know the age of the buildings. In such cases, estimates were made and checked afterward whenever possible. Errors of estimate on old buildings are of little significance. Likewise many farmers, especially if they had purchased their places within a year or two, could not give yields of crop for a few years. Yields for three years, however, were obtained in most cases.

Altho the Tax Commission records show 379 bona fide sales in Blue Earth County from 1916 to 1919, only 160 farms were covered

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[7] Access to the sales data files of the Minnesota State Tax Commission was given us through the courtesy of the Tax Commission.

[8] We also asked each farmer the purchase price of his farm as an additional check. In only two instances did the purchase price given by the farmer disagree with the sale price on record. The difference in these two cases was only about $200 on $20,000 sales.

in the survey. Figures 1 and 2 show that these 160 farms are well distributed both as to location and soil types.

Method of analysis.—Altho it is not the province of this treatise to explain the theory of multiple or partial correlation, some discussion of its use is needed at this point. If in two series of variables—for example, in this case, cost of buildings per acre and value per acre—a high value of one tends to be associated with a high value of another, the variables are said to be correlated and the correlation is positive; while if a high value of one is associated with a low value of another, as in the case of distance to market and value per acre, the correlation is negative. The best numerical measure of the amount of correlation is called Pearson's coefficient of correlation. The algebraic formula for this is:

$$r_{12} = \frac{S\,X_1 \cdot X_2 - N \cdot M_1 \cdot M_2}{\sqrt{(S\,X^2_1 - N \cdot M^2_1)\ (S \cdot X^2_2 - N \cdot M^2_2)}}$$

In a problem in which more than two factors are concerned, the simple or gross correlation may be an expression only of an apparent relationship. This apparent correlation may be due to the fact that each of the two variables or factors is correlated with another or several variables. For example, assume in this case that distance to market and value per acre show a negative correlation, but as distance from town increases the percentage of land of desirable grade decreases, or in other words, that there is also a negative correlation between distance to market and the percentage of land of desirable grade. The gross or apparent negative correlation of distance to market and value per acre is partly due to the fact that as the distance from market increases, the percentage of land of desirable grade becomes smaller, this operating to make the farms more distant from market sell cheaper, not due to distance alone as the simple coefficients might lead one to believe.

In a problem of the type that land-appraising presents, where the relationship between several variables or factors must be considered simultaneously, a coefficient of net or partial correlation is calculated. Thus if we are considering four variables, 1, 2, 3, and 4, the partial coefficient of correlation $r_{12\cdot34}$ means the net relationship between variables 1 and 2 when the effect of factors 3 and 4 are held constant.

When three variables are considered, the partial correlation $r_{12\cdot3}$ may be calculated from the formula:[9]

$$r_{1\cdot23} = \frac{r_{12} - r_{13} \cdot r_{23}}{\sqrt{1 - r^2_{13}} \cdot \sqrt{1 - r^2_{23}}}$$

By further expansion, the formula for five variables as used in this problem is:

[9] Yule, G. U, "An Introduction to the Theory of Statistics." 5th ed. 1919.

$$r_{15.234} = \frac{r_{15.34} - r_{12.34} \cdot r_{25.34}}{\sqrt{1 - r^2_{12.34}} \cdot \sqrt{1 - r^2_{25.34}}}$$

From the coefficients of correlation, we can determine the coefficients of relationship expressed in absolute units, known as coefficients of regression: for example, $b_{15.234}$ (σ representing standard deviation).

$$b_{15.234} = r_{15.234} \frac{\sigma_{1.5234}}{\sigma_{5.1234}}$$

The forecasting formula is readily determined when once the regression coefficients are known. Following is the generalized formula:

$$X_1 = a + b_{12.345} \cdot X_2 + b_{13.245} \cdot X_3 + b_{14.235} \cdot X_4 + b_{15.234} \cdot X_5$$

(X_1 represents value per acre in this case, and X_2, X_3, X_4, X_5, the other factors considered.)

The probable error involved in predicting X_1 from the other factors is expressed in the formula:

$$\sigma_{1.2345} = \sigma_1 \sqrt{(1 - r^2_{15})} \sqrt{(1 - r^2_{14.5})} \sqrt{(1 - r^2_{13.45})} \sqrt{(1 - r^2_{12.345})}$$

Probable error $= \sigma_{1.2345} \times 0.674489$

These equations and explanations are presented so that the reader will be familiar with the notations when they are used later.[10]

Value per acre.—The problem under value per acre is to reduce the sale prices of sales made during a four-year period, during which prices were rising rapidly, to a comparable basis. First we must make sure that the relative distribution of grades of land sold in the different years was the same. The statistical measure best adapted to show this is the "coefficient of variation," solved by the formula:[11]

$$V = 100. \frac{\sigma}{M}$$

The coefficient of variation in the fourth column of Table II shows that the distribution of grades of land was very similar during the four years. The average sale prices per acre for the four years, given in the second column, are, therefore, closely comparable. The third column reduces these prices to indices, base year 1919. The sale prices of the farms bought in 1916, 1917, and 1918 were raised to 1919 level by dividing them by the index number for that year as given in this table. Thus a farm sold for $150 per acre in 1917 would have sold for $189.49 per acre in 1919 ($150÷.79157). This method introduces

[10] Persons interested in the technique of the method are referred to G. U. Yule's "On the Theory of Correlation for Any Number of Variables Treated by a New System of Notation." Proceedings Royal Society, Series A., Vol. LXXIX 1907, p. 182; also to Yule's "An Introduction to the Theory of Statistics."

[11] Yule, G. U. "An Introduction to the Theory of Statistics." 5th ed. 1919. Pearson, Karl, "Chances of Death."

some error into the calculations because it divides each sale price by the average for the whole year. It is likely that prices in January and December will, during a period of rising prices, be respectively below and above the average. This error will be greatest in 1919. The only method of correcting for this is to get indices by months. This can be done in surveys made in the future.

TABLE II

YEARLY AVERAGE SALE PRICE PER ACRE, INDICES OF SAME, AND COEFFICIENT OF VARIATION FOR EACH YEAR

Year	Average sale price	Indices	Coefficients of variation
1919	$157.23	100.000	24.135
1918	134.96	85.837	26.250
1917	124.46	79.157	25.618
1916	114.52	72.836	25.557

Differential for state macadam and dirt roads.—The differential for dirt and macadam roads was determined by cross-tabulation. In the final results, lands on macadam roads were reduced to a dirt road basis. Following is the solution of the problem: First of all, a simple tabulation gave the following results:

Average value per acre of 10,393 acres on dirt roads =$147
Average value per acre of 4,873 acres on state roads = 171

Differential .... $ 24

Tables III and IV test the validity of this differential by cross-tabulation. The assumption basic to this method is that if $24 is a true constant difference between state and dirt roads, it should appear also in any cross-tabulation of data on the basis of other factors, provided the acreage included in each class interval is large enough to allow the effects or the influence of the other factors to average out or compensate. In Table III, a constant difference of about $20 appears in the classes where the distribution is large: for example, in the class interval "Cost of buildings, $0-$12"—dirt roads, $131, and state roads, $153; and also in the class $12-$24—dirt roads, $152, and state roads, $173. In the other classes in this table, the number of acres is too small to furnish evidence as to the genuineness of the differential. Similarly in Table IV, the cross-tabulation on the distance-to-market basis, the differential of about $20 again occurs in the classes having the large distributions; for example, in class interval 0-2.5 miles—dirt roads, $160, and state roads, $180; and class 2.5-4.5 miles—dirt roads, $155, and state roads, $173.

TABLE III

CROSS TABULATION ON BASIS OF STATE AND DIRT ROADS AND COST OF BUILDINGS PER ACRE

	Dirt Roads			State Roads	
Cost of buildings per acre	Value per acre	Acres	Cost of buildings per acre	Value per acre	Acres
$ 0–$12	$131	4,949	$ 0–$12	$153	1,492
12– 24	152	4,037	12– 24	173	2,164
24– 36	182	1,058	24– 36	189	733
36– 48	. . .	. . .	36– 48	164	176
48– 60	213	349	48– 60	194	277
60– 72	. . . .	. . .	60– 72	. . . .	. . .
72– 84	. . .	. . .	72– 84	349	30

TABLE IV

CROSS TABULATION ON BASIS OF STATE AND DIRT ROADS AND DISTANCE TO MARKET (MILES)

	Dirt Roads			State Roads	
Distance to market	Value per acre	Acres	Distance to market	Value per acre	Acres
0– 2.5	$160	2,546	0– 2.5	$180	1,498
2.5– 4.5	155	4,104	2.5– 4.5	173	2,309
4.5– 6.5	133	2,161	4.5– 6.5	203	210
6.5– 8.5	131	1,352	6.5– 8.5	138	712
8.5–10.5	127	155	8.5–10.5	189	40
10.5–12.5	78	75	10.5–12.5	169	102

From the results in Tables III and IV, a weighted average differential for state roads was determined. Only the differentials appearing in the largest two classes in these tables were used. These were weighted according to number of acres in the class. For Table III, this gave a weighted difference of $24.44 per acre; for Table IV, $18.87 per acre. These two averaged according to acreage weights gave $21.92 as the weighted average differential.

There are, however, 3,743 acres of land located on dirt roads, and 1,062 acres located on state roads, at distances farther from town than the classes used in obtaining the $21.92 differential, at distances ranging from 4.5 to 12.5 miles from town, which might have a widely different differential. However, when they are thrown together so as to give enough for a sample, the difference is only $26 per acre, $156 per acre for the land on state roads, and $130 for the land on dirt roads.

The $21.92 differential is further substantiated by separating farms on dirt and state roads and correlating each group with distances to market. The following forecasting equation results:

X = price per acre; Y = distance to market

State roads: $X = 187.29 - 7.04 Y$

Dirt roads: $X = 161.47 - 5.05 Y$

If this equation is applied to farms at various distances from market, e.g., 1.25 and 3.75 miles, the following prices result:

1.25 miles—state road, $178.49; dirt road, $155.16; difference, $23.33

3.75 miles—state roads, $160.89; dirt road, $142.53; difference, $18.36

Average difference $20.85

Again, after the values per acre of the farms on state roads were corrected by means of the differential $21.92, all the farms adjacent to Class II towns[12] were sorted out and classified on the basis of state and dirt roads. The 5,842 acres on dirt roads when thus corrected averaged $144.48 per acre, and the 2,433 acres on dirt roads $144.74 per acre. This indicates that the correction $21.92 must be very nearly right.

Again, when farms on state roads and dirt roads were correlated separately as to price per acre and distance from market, the coefficients of correlation were $r = -394$ and $r = -240$ respectively. After the values of farms on state roads were corrected by the $21.92 differential, and the values of all farms together correlated with distance from market, the coefficient was $r = -.230$, just .01 from the $-.240$ coefficient. Here again the $21.92 differential is substantiated. In the remaining calculations, therefore, the farms have all been converted to the dirt-roads basis according to this differential.

In this connection, it should be understood that the higher value of the land on state roads is due to the fact that such roads are, and always have been, main lines of travel, as well as to the quality of the road.

Differential for influence of cities and villages, markets, etc.—The cities and villages in the area were put in two classes on the basis of population and market facilities, Class I including Mankato, Lake Crystal, and Janesville, and Class II including all small towns of about 500 population.

The correction for the influence of Class I towns on land values was worked by cross-tabulation in the same manner as the differential for roads. The average value per acre of 3720 acres adjacent to Class I towns was $158.36; of 8290 acres to Class II towns, $143.98. This gives a difference of $14.37 per acre. Cross-classifications were made to test the validity of this $14.37 as a true constant difference. Table V shows that the remaining factors affecting land prices average nearly the same for Class II towns.

[12] Small towns of about 500 population.

TABLE V

AVERAGE VALUE OF FACTORS IN EACH CLASS OF TOWNS

Factors	Class I	Class II
Cost of buildings...	$15.52	$12.71
Productivity index	99.7	95.0
Land-classification index	86.9	85.5
Distance to market, miles.................................	3.96	3.45

Analyzed further, the following results appear:

A. For all farms located 2½ to 4½ miles from market, with productivity indexes between 89 and 100, the price of the land averaged for—

    Class I towns.................................... 165.03 (1,299 acres)
    Class II towns................................... $152.60 (903 acres)

        Difference .... $ 12.43

B. For all farms where cost of buildings per acre ranged from $12 to $24 per acre, the prices of land averaged for—

    a. Productivity indexes between 76 and 90 and —

        Class I towns............................. $161.84 (507 acres)
        Class II towns............................ 151.48 (701 acres)

        Difference .... $ 10.36

    b. Productivity indexes between 90 and 104 and —

        Class I towns............................. $155.64 (817 acres)
        Class II towns............................ 138.94 (1,486 acres)

        Difference .... $ 16.70

    c. Productivity indexes between 104 and 118 and —

        Class I towns............................. $166.52 (542 acres)
        Class II towns............................ 154.52 (1,076 acres)

        Difference .... $ 12.00

The average of the differences in *a*, *b*, and *c*, weighted on the basis of average, is $13.72.

C. For all farms on dirt roads, the price of the land averaged for —

    Class I towns.............................. $157.19 (2,915 acres)
    Class II towns............................. 144.48 (5,842 acres)

        Difference .... $ 12.71

The average of the differences in A, B, and C, weighted according to acreage, is $12.82. This was used to convert all Class I towns to a Class II basis.

At this stage in the analysis, all farms have been reduced to the following basis: Sold in 1919; on dirt road; adjacent to Class II towns. The four remaining factors influencing land prices, namely, cost of buildings per acre, type of land, productivity of soil, and distance to market, will be handled by partial correlation methods.

Calculation of 1919 depreciated cost of buildings.—The dimensions and type of structure of each building were obtained in the field. From the dimensions, the cubic-foot content of each farm structure was calculated. This was then multiplied by a certain cost per cubic foot depending on the type and kind of structure. This cost was then depreciated down to the year 1919. The depreciation rate used was

based on the condition of repair of the building and its age. Cost of buildings was reduced to an acre basis before being used in the correlation. The following is a sample of the calculations for one farm:

TABLE VI

SAMPLE CALCULATIONS OF BUILDING COST

Building	Cubic feet	Cost per cubic foot	Cost	Depreciation to 1919	Depreciated cost 1919
Dwelling	11,520	$.14	$1,612.80	38%	$999.94
Barn	16,456	.05	822.80	51%	403.17
Hen house	3,500	.05	175.00	80%	35.00
Machine shed	4,000	.03½	140.00	80%	28.00
Milk house	1,260	.05	63.00	51%	30.87
Granary	4,480	.05	224.00	28%	161.28
Corn crib	7,500	.03½	262.50	80%	52.50
Shed	2,160	.05	108.00	28%	77.76

Total 1919 depreciated cost.. $1,788.52

The cubic-foot costs used are given in Table VII. Silos were each considered separately because of varying types of construction.[13] For depreciation tables used, see Appendix B.

TABLE VII

BUILDING COST PER CUBIC FOOT

Type of building	Cost per cubic† foot in 1919
	Cents
Dwellings, frame, small box house, no cornice..........................	9½
Dwellings, frame, shingle roof, small cornice, plain.....................	12 to 14
Dwellings, brick, same class..	16½ to 19
Dwellings, frame, shingle roof, good cornice, sash weights, good house..	16½ to 19
Dwellings, brick, same class, good house...............................	21½ to 24
Barns, frame, shingle roof, not painted, plain finish...................	3½ to 6
Barns, frame, shingle roof, painted, good foundation...................	6 to 7
Single corn crib*..	4
Double corn crib*...	3½
Machine shed*..	3½

* Calculated by the writer.

† Wm. Arthur. "New Building Estimator," p. 311. Prices for 1902 were raised to the 1919 level by using the U. S. Bureau of Labor indices of building material prices, and wages of carpenters, bricklayers, painters and common laborers. Bulletins Nos. 269 and 77, U. S. Bureau of Labor.

Land-classification index.—The percentage of each type of land could have been entered directly in the multiple correlation equation, but not without increasing the required calculations many fold. Hence, all the grades were reduced to a common denominator and expressed in one figure, which was called the land classification index. This was calculated by weighting the percentage of each class of land by a figure

[13] Ibid. Silo cost data—p. 535-555.

representing its approximated relative value significance. The weights used were :[14]

                                                                    Weights
  Grade 1. Woods—not potentially tillable[15]............ 1/5
  Grade 2. Woods—potentially tillable· 1/2
  Grade 3. Wild hay land............................... 3/4
  Grade 4. Tillable 1

Following is an illustration of how this method was applied to a given farm. The 10 per cent of Grade 1 land was multiplied by the weight 1/5, etc. The index for this farm is 82.

Grade	Per cent	Weights	Index
Grade 1....................	10	1/5	2
Grade 2....................	· 10	1/2 .	5
Grade 3....................	20	3/4	15
Grade 4....................	60	1	60
Land Classification Index...			82

Productivity-of-soil index.—The productivity index is a relative figured on the basis of the average yields of the principal crops grown in Blue Earth County. The crops were considered of equal weight. The index for each farm is the average ratio of the three-to-five year average crop yield of the farm to the average crop yield of the county. Ordinarily it would be well to weight the different crops according to their importance, but in this case the crops were of about the same importance.

TABLE VIII

ILLUSTRATION OF CALCULATION OF PRODUCTIVITY INDEX FOR ONE FARM

Crops grown	Average yield per acre	County average yield per acre	Per cent of county average yield
Corn, bu...........................	65	48.23	134.7
Oats, bu...........................	55	41.26	133.2
Spring wheat, bu..................	18	12.53	143.5
Clover and timothy, tons..........	2	2.18	91.5
Productivity-of-soil index			125.80

[14] The weights were approximations resulting from judgments based on the observation of sales of the various grades, and on data in Minnesota Bulletin 145, "The Cost of Producing Minnesota Farm Products"; Minnesota Special Bulletin No. 19. "Cost of Milk Production"; Minnesota 1920 Census; and the Crop Reporter, Dec., 1919. The weight 3/4 placed on wild hay land may seem a little large; but this was usually good low land which could be tiled. It was not tiled, however, because the farmers found that especially in dry seasons the wild hay crop would compensate for the short crop of tame hay.

[15] Includes other not potentially tillable land which can be pastured.

Distance to market.—The distance to market was obtained by asking the farmer the question, How far is it to the town where you market most of your products?

The correlation.—The following five factors were then considered in multiple correlation:

X_1 = Value per acre corrected as previously explained.

X_2 = 1919 depreciated cost of buildings per acre.

X_3 = Land classification index.

X_4 = Productivity of soil index.

X_5 = Distance to market.

The forecasting equation which resulted is:

$$X_1 = +57.785 + 1.067 \cdot X_2 + .7279 \cdot X_3 + .1658 \cdot X_4 - 3.422 \cdot X_5$$

It is interesting to note some of the relationships brought out by the equation. An increase in a dollar's worth of buildings per acre increases the land value $1.07 per acre. This is a very significant result, as it substantiates the general practice of adding the depreciated cost of buildings to the land value in order to secure the value of the farm real estate. It also indicates the relative accuracy of the method used in this investigation for calculating the depreciated building costs. An increase of one point in the land classification index results in a rise in the value per acre of 73 cents. In this area the productivity-of-soil index was the least significant factor studied. An increase of one point in this index results in a 17 cent increase in the value per acre. This index merely indicates soil productivity differences, most of the land variation being indicated by the land-classification index. The most interesting and yet the most difficult relationship to study was that of distance to market and value per acre. Coupled with this relationship is the relative significance of the type of road and class of town. On a farm which is on a dirt road and adjoining a Class II town, each mile from town decreases the land value per acre $3.42.

The extreme range in value of buildings per acre is from nothing, on 40 pieces of land, to $83; the ordinary range is from $5 to $35 per acre, and the modal group is from $10 to $20.

The land-classification index ranges from 25 to 100 (on 25 farms), and all but 31 farms have an index of 75 or more. A farm with an index of 75, other things being the same, will be worth $18.20 less per acre than one with an index of 100, and one with an index of 50 will be worth $36.39 less. The extreme range in productivity indices is from 60 to 140, and the ordinary range from 80 to 120. A farm with a productivity index of 80, other things being the same, is worth $6.63 less per acre than a farm with an index of 120.

Half of the farms were between 2 and 5 miles from market; 20 more were between 5 and 7 miles, and 22 more between 7 and 9 miles; 19 were less than 2 miles from market. Other things being the same,

the farm farthest from market, 11½ miles, is worth $35.92 less per acre than the farm a mile from market.

Following are two illustrations of the use of the forecasting equation:

No. 1. Farm sold in 1918 for $150 per acre—state road, Class I town:

$X_2 =$ 1919 depreciated cost of buildings per acre...... $36.24

$X_3 =$ Land-classification index 87

$X_4 =$ Soil-productivity index 95.5

$X_5 =$ Distance to market........................ 9 miles

$X_1 = 57.785 + 1.067\ X_2 + .7279\ X_3 + .1658\ X_4 - 3.4219\ X_5$

$X_1 = 57.785 + 38.668 + 63.327 + 16.016 - 30.797$

$X_1 = 144.999$

    $+21.92$ state road correction

    $+12.82$ "Class I" town correction

    _____

    179.739

    $\times .8584$—1918 land-value index

    _____

    154.28 =estimate. 150=actual sale price.

No. 2. Farm sold in 1919 for $135 per acre—dirt road, Class II town:

$X_2 =$ 1919 depreciated cost of buildings per acre....... $12.47

$X_3 =$ Land classification index...................... 75.62

$X_4 =$ Soil productivity index...................... 103.7

$X_5 =$ Distance to market........................3.5 miles

$X_1 = +57.785 + 1.067\ X_2 + .7279\ X_3 + .1658\ X_4 - 3.4219\ X_5$

$X_1 = +57.785 + 13.305 + 55.043 + 17.193 - 11.976$

$X_1 = 131.35 =$ estimate. $135 =$ actual sale price.

The multiple correlation between one variable, such as land sale prices, and several other variables, such as the four value factors, is expressed by R, which in this case equals .81. If these four factors alone accounted for all the variations in sale prices, R would be 1.00. Statisticians consider an analysis giving a result as high as .81 as reasonably successful.

Appraisal by means of this equation involves a probable or average error of 9.55 per cent of the average sale price, or $15 per acre. This means substantially that one half of the appraisals would be less than 9.55 per cent in error, and that the other half would have more error than this.

The forecasting equation was applied to each farm in the survey and the results checked against the sale prices. A frequency table of the differences shows that 24 farms are within $5 of the sale price, and 22 more within $10 of the sale price. On the other hand, there are 13 farms more than $30 too low, and 21 farms more than $30 too

high. When these farms are examined, certain deficiencies in the present survey become apparent.

First, it is evident that the method of reducing the sale price to the 1919 basis by indices based on the average of the year's sales, has introduced considerable error, especially in farms sold in 1919 when the land boom was getting under way. This is obviously the largest source of error. This error can be eliminated largely in future surveys. (See page 14.)

Second, it is evident that the land classification index was crude and based on insufficient evidence. The proper method is to include the proportions of the different classes of land as variables in the multiple correlation analysis. Each class of land will then be represented by a member in the forecasting equation. This error showed especially in pieces of land with no buildings upon them, which sometimes were nothing but meadows or timber lots.

Third, special circumstances affecting many of the farms were not included in the analysis. Among these are location close enough to a city to give the land prospective value as sites for city residences. Another is location on a lake front. Future surveys may omit these farms, or else include enough of them to permit the special circumstances involved to be included in the equation.

Fourth, the yield data did not cover a long enough period. A systematic use of this method would give data over a constantly increasing number of years. Furthermore, the yield of crops is dependent in part upon the ability of the farmer, and the part of the yield thus determined is only to some extent reflected in land values. Yield of crops is, therefore, not a satisfactory basis for a productivity-of-soil index. However, it is probably the best basis at present available.[16]

The equation, however, gives relatively small weight to productivity in so far as it is not included in land classification.

It is likely that the productivity of the land in producing pasturage for dairy and beef cattle and sheep should figure in the index wherever these are important farm enterprises. Also, as already pointed out, the various crops should be weighted according to their importance on any farm.

After all these improvements have been introduced into the method, there will still be a difference between the actual sale price of any farm and that which the equation would indicate. The primary reason for this is the disorganization of the land market already discussed. The same quality of land does not sell for the same price at the same time. Many sales are made at prices too high or too low. In this respect, the values indicated by the equation will be more accurate

[16] If the methods outlined in this bulletin are ever used in assessing land, there will, of course, be serious objections to using yields as a factor in values.

than the actual sale prices. The other error remaining will be due either to errors in the measures used for productivity, land classification, value of buildings, class of town or type of road, or to the presence of other factors affecting land values on certain of the farms.

It is not unreasonable to believe, however, that the probable error can be reduced under 5 per cent, perhaps under 3 per cent, in areas when the land is as uniform as in Blue Earth County. A probable error of 3 per cent would mean that half the appraisals were within less than $4.70 per acre of the sale price. If this could be accomplished, the appraised value would undoubtedly be a safer measure of value than actual sale price on a majority of farms. In other words, it would mean that the errors in this method were less than the errors caused by the disorganization of the land market.

In areas where land is less uniform in type and quality, it is not likely that as accurate an equation can be obtained.

APPLICATIONS

The method of appraisal here outlined can be of great practical value for many purposes, chief of which are the following: (1) as a basis for mortgage loans; (2) as a basis for assessment and taxation; (3) as a basis for buying and selling; (4) for inventorying a farm business or an estate; (5) as a basis for estimating rent on different farms and different classes of land where rents are needed for cost accounting; (6) as a basis for determining benefits and damages from drainage ditches, roads, and other local improvements; (7) as a basis of settlement of court disputes involving questions of land values; (8) for making valuation of farm land used in railway right-of-ways and the like.

The Federal Land Banks, the joint stock land banks, other banks, mortgage companies, insurance companies, and others who loan money on farm land are in need of a scientific measure of farm land value such as is here presented. Land credit can not be put on an equitable basis unless farm values are appraised accurately. The lack of this value information is the principal reason for our present "conservative" policy, for with underestimated valuations and with his security thus understated, the farmer is not able to get all the credit he desires. This is not only of interest to farmers, but also to the investors. The investor wants to be certain that the values placed on the mortgaged land are their true values. If the investing public was convinced that such valuations represented true market values, it would no doubt accept a lower net yield on the investment in lieu of the decreased risk due to accurate appraisal. Accurate appraisal would thus bring about lower interest rates to farmers on long-time credit.

It would be comparatively easy for the Federal Farm Loan system to use the methods here outlined once they were perfected. First of all, the territory of the United States would need to be blocked out into large areas where conditions are similar. In each of these, a survey would need to be made including preferably 1000 farms located in several representative counties in various parts of the area. The factors selected as influencing land values would be somewhat different for the different areas. The forecasting equation obtained could be applied to all the farms in the area except a small number with pronounced characters not represented in the equation. The same equation could be used by insurance companies, farm mortgage companies, and even local banks. Of course the smaller the area included in the survey, the more uniform conditions are likely to be and the more dependable the equation.

The assessed valuations of the 160 farms covered in the survey have the amazing probable error of 26.7 per cent of the average sale value, or $33 per acre, compared with the probable error of 9.55 per cent of the average sale value, or $15 per acre, in the results obtained in this survey. A probable error of 26.7 per cent means substantially that half the assessed valuations are more than $33 per acre above or below the sales price. If nothing more had been done than to apply the average sales price, $157.23 per acre, uniformly to all farms, the probable error would have been only 16.4 per cent, or $25.76 per acre.

This method of analysis of assessed values sets up sales prices as the standard, and all departure from this is considered as an error. From the standpoint of the state as a whole, and on the assumption that all forms of property, city real estate, railroads, mines, etc., can be and are assessed at full current values, this method of analysis is correct. Also from the point of view of distributing state taxes equitably between the various counties of the state, either all farms should be assessed at current market value, or else all on some other uniform basis that gives equal departure from it in all counties. It is hard to conceive of any workable standard other than current market values.

However, from the point of view of treating all farms in a county alike, the foregoing analysis does not fit. Of the error of $33 per acre, $11 was due to the fact that land is in general assessed too low. If the level of assessed value is set up as the standard, and departures from this are considered as error, then the probable error is $21 per acre, or 17.3 per cent of the average sale value at the time of assessment. The percentage figure is the proper basis of comparing. This 17.3 per cent is to be compared with 16.4 per cent probable error if the average sales price had been applied uniformly to all the farms, or 9.55 per cent if the method of appraisal outlined in this bulletin had been used, and

perhaps under 3 per cent if this method were further developed and the equation expanded to include more variables.

The method of appraisal here outlined could be generally used for purposes of assessment. Ordinarily the county would be the unit, altho it might be advisable to section the county if it had two or more distinct types of soil, topography, and agriculture. To start with, the first year under the new method the assessors in their regular visits would fill out a schedule much like the one in Appendix A. In succeeding years, all the additional information which they would get would be yields during each preceding year, and dimensions and descriptions of new buildings and other improvements. From the assessor's reports, the farms sold within recent years would be selected, and the data on the assessor's schedules for these farms used in a correlation analysis with the recorded sales prices now regularly obtained. This would give an equation which could be applied to all farms in the county. The actual assessing of land values could be done in the office of the State Tax Commission. Once the equation was obtained it would be used year after year simply by correcting it to fit the changes in land values indicated by the sales records. A recalculation of the equation after several years would, however, be desirable so as to make use of the gradually accumulating yield data.

There would be some extra expense involved in getting the new system under way. The assessor's work would be heavier the first year. The calculating of the equation the first year would take two or three persons perhaps a month. But once the system was under way, it is doubtful whether it would entail any greater expense. After the first year, the work of the local assessors would be simplified and reduced. It is quite likely that similar methods could be used in valuing livestock and equipment. In the end, therefore, there might be very little for the assessor to do. He would become a sort of enumerator, all valuations being made by the Tax Commission. Assessments could then be taken entirely out of politics. Farmers would know that their farms were being assessed on a strictly objective, scientific basis with no possible chance for favoritism or prejudice.

Using this method, the State Tax Commission could at one stroke attain the "full and true" value assessment which is so difficult with local assessors making the valuations.

What is even more important, once the significance of the various factors influencing land values was determined, taxes could be levied more equitably and intelligently. For example, road expenses could be distributed according to road benefit. Location value could be taxed at a different rate from buildings or productivity value.

Closely related to the foregoing, is the use of the method to determine benefits and damages from drainage ditches, roads, and other local improvements. Equations already developed for general taxation purposes would be sufficient in some cases; in others, special surveys would need to be made.

There are many farm real estate agencies with enough business to warrant their using these methods. But the only use made of them need not be in buying and selling land. The real estate men in a county can with advantage organize a county real estate board and equip it to render this appraisal service to its members and to the public in general. City real estate boards have found that such a service helps their members to make sales because it reassures buyers. This county board would obtain all needed information concerning each farm as it was sold, and on the basis of this develop an equation. If it wished to begin appraising at once, however, it would need to make a survey of past sales.

The general use of this system by real estate men and buyers and sellers of land would have the same effect on the land market that setting up market grades has had on the grain and livestock markets. It would, therefore, be of great public benefit. It might even be possible to quote prices on various grades and types of land.

In all surveys for the purpose of studying farm organization, the placing of values on the farms has been one of the difficult problems. An analysis of the valuations made in two surveys by the Office of Farm Management of the United States Department of Agriculture has shown a high probable error. This error, however, has not been of much significance so far as the conventional type of farm business analysis is concerned. But there are analyses that should be made in which this error would be a serious handicap.

Farm cost-accounting studies frequently need valuations of different types of land in one farm. This method could be made to supply these valuations.

With so many agencies having need of the results of such analysis and appraisals, it would seem foolish for each to undertake the task independently. Some public agency, such as the Tax Commission, could do the work for all. All that the land banks or insurance companies, or a real estate board would then need would be an organization to apply the results.

APPENDIX A

SCHEDULE

LAND:			No. of farm_____
Acres in purchase.....................	_____		Name of owner_____
Woods not pastured..:.............:.	_____		Date of purchase_____
Potentially tillable_____		XXXXX	Distance to market_____
Woods pastured.....................	_____		Name of market_____
Potentially tillable_____		XXXXX	Type of road_____
Other non-tillable pasture............	_____		Rods frontage_____
Rough_____ Wet_____ Stony_____		XXXXX	Topography _____
Til'able pasture.....................	_____		
Wild hay land ( )	_____		Soil types_____
Other tillable land...................	_____		Remarks _____
Waste land ( )	_____		
....	_____		

BUILDINGS:	Dimensions	When built	Construction cost	Condition	Type of construction	Remarks
Dwelling						
Barn						
Hog barn....						
Hen house...						
....						
....						
....						
Granary						
Corn crib....						
....						

CROPS: Yields

Year	Corn	Silage	Oats	Barley	S. Wheat	W. Wheat	Rye	Pota- toes	Wild hay	Tame hay
1920										
1919										
1918										
1917										
1916										

INSTRUCTIONS FOR USE OF THE SCHEDULE

1. Number each schedule with the number which appears on the county map and sales-transfer card.

2. Check the "acres in purchase" against the seven classes of land listed, namely, "woods not pastured," "woods pastured," "other non-tillable pasture," "tillable pasture," "wild hay land," "other tillable land," and "waste land."

3. The classification is so arranged that tillable land can be separated from all non-tillable land; also pasture land from crop land and woods. These totals can be worked out later.

4. Under "non-tillable pasture" indicate by a check mark whether it is non-tillable because of roughness, wetness, or stones. If there are two or more reasons, indicate the number of acres accounted for by each.

5. "Wild hay land" will include meadow too wet to be plowed, and, in some cases, land too rough to be plowed. Indicate in the parenthesis following the reason the land is kept in wild hay.

6. Indicate in the parenthesis after "waste land" the nature of the waste land. The part of the waste land which is caused by roads can be estimated from the "rods frontage" listed in the next column.

7. Fill in the name of owner and date of purchase before visiting the farm.

8. In a few cases you will find that the farm you visit has been sold since your last record of transfer. If you can get the farmer to tell you the amount of the transfer, it will be worth while for you to take the record as of the latest date.

9. Under "rods frontage" count up the number of rods of road taken out of the farm. If the road passes through the farm, the rods will need to be doubled, because in this case four square rods will be taken out for each rod of road in place of two square rods.

10. Under "soil types" indicate the soil type as described in the soil map of Blue Earth County. If a farm has more than one soil type, indicate the relative proportions of each. This will require that the farm be located rather definitely on the soil map. This can probably be done by matching the soil map against the plat book map. This work can be done mostly after you get home.

11. Under "remarks" mention any unusual circumstances, such as stony land, floods, poor drainage, run-down soil, land improvements, etc.

12. "Construction cost." Obtain the cost of original construction of a building whenever the farmer happens to know what it is.

13. "Condition." In general, describe the condition of the building as "very good," "good," "fair," "poor," or "very poor." Abbreviations may be used for these terms.

14. Under "remarks" enter any special circumstances connected with the construction of any of these buildings, such as sanitary barn equipment, etc.

15. Express the "yields" of the various crops in their usual units, i. e., corn in bushels per acre, silage in tons per acre, etc. Get data as to yields from any available source that you can. Very frequently the farmer who is on the place will not know very much about the yields made by his predecessor. If necessary, get the desired information from the neighbors, threshermen, etc.

16. The classification "tame hay" may mean red clover, alfalfa, timothy, or timothy and clover mixed. It might be well to indicate which is referred to, by some form of abbreviation.

APPENDIX B

TABLE I
DEPRECIATION TABLES FOR FRAME DWELLINGS*

Years	Percentage depreciation according to condition		
	Good	Fair	Bad
	Per cent	Per cent	Per cent
1	3	4	10
2	6	7	17
3	8	10	23
4	10	12	27
5	13	15	31
6	15	17	34
7	17	19	37
8	18	21	40
9	20	23	42
10	22	25	45
11	23	26	47
12	25	28	49
13	26	30	51
14	28	31	53
15	29	32	55
16	30	34	57
17	31	35	58
18	32	36	60
19	33	37	61
20	34	38	63
21	34	39	65
22	35	40	66
23	36	41	68
24	37	42	69
25	37	43	71
26	38	44	72
27	39	45	74
28	39	46	75
29	40	47	79
30	41	48	80
31	41	48	80
32	42	49	82
33	42	50	83
34	43	51	85
35	43	52	86
36	44	53	88
37	45	53	90
38	45	54	91
39	46	55	93
40	46	56	95
41	47	57	. .
42	47	59	. .
43	48	59	. .
44	48	59	. .
45	49	60	. .
46	50	61	. .
47	50	61	. .
48	51	63	. .
49	51	64	. .
50	52	64	. .

* Used in Cleveland Valuation, published in "New Building Estimator" by Wm. Arthur.

TABLE II

DEPRECIATION TABLE FOR BRICK DWELLINGS

Years	Depreciation
Per cent	Per cent
1	5
2	7
3	9
4	11
5	13
10	18
15	23
20	28
25	33
30	39
35	45
40	50
50	60
60	70
70	80

TABLE III

DEPRECIATION TABLE FOR BARNS, GRANARIES, AND OTHER FARM BUILDINGS*

Years	Depreciation rate according to condition		
	Good	Fair	Bad
	Per cent	Per cent	Per cent
1	10	12	14
2	12	15	17
3	14	18	20
4	16	21	23
5	18	23	26
6	20	26	29
7	22	29	32
8	24	32	35
9	26	35	38
10	28	38	41
11	30	41	44
12	32	43	47
13	35	47	53
14	38	51	59
15	41	55	65
16	43	59	71
17	46	63	77
18	49	67	83
19	52	71	..
20	55	75	..
21	58	79	..
22	61	81	..
23	64	..	..
24	67	..	..
25	70	..	..
26	73	..	..
27	76	..	..
28	79	..	..
29	82	..	..
30	..	..	..

* The Bernard Depreciation Table, "How to Assess Property in Cities and Rural Towns." In report of the Wisconsin Tax Commission, 1914, p. 32. H. V. Cowles and J. H. Leenhouts.

The University of Minnesota
Agricultural Experiment Station

Factors Determining the Price of Potatoes in St. Paul and Minneapolis

By Holbrook Working

Division of Agricultural Economics

UNIVERSITY FARM, ST. PAUL

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CONTENTS

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FACTORS DETERMINING THE PRICE OF POTATOES IN ST. PAUL AND MINNEAPOLIS

By Holbrook Working

FOREWORD

Most of the readers of this bulletin will find in it certain sections in which they are more especially interested than in others. Growers of potatoes and dealers will find the latter part of the bulletin, beginning with the section on "Use of the Price-Forecasting Formula" (p. 27) of most immediate practical value. The sections on "Description of the Market" and "Considerations Influencing Dealers" (p. 4-8) will be found of almost equal practical value. Growers and dealers who wish to get a better understanding of the fundamental forces which influence price will find it profitable to read the two sections on the various factors which do and do not measurably influence price (p. 15-27).

Economists will be especially interested in the first four sections following the "Summary" (p. 4-15), and in the discussion of the factors which do and do not measurably influence price. Those who wish to study the basis for the results with special care will make use also of the section on "Source of Price Statistics" (p. 10-15).

Most of the methods used in the study are familiar to those who have followed recent developments in the use of partial correlation for the study of time series, as developed chiefly by Professors Warren M. Persons, H. L. Moore, and G. Udney Yule. In some points the methods used by these investigators have been further developed or supplemented by original methods. A technical discussion of the methods used will be published in a later bulletin designed for the use of investigators. Pending its appearance, the writer will be glad to make any necessary explanations for the benefit of any one who may wish to make a similar study for another market.[1]

SUMMARY

An extended study of the price of potatoes in Minneapolis and St. Paul appears to have resulted in the discovery of all the important fundamental factors determining the price of potatoes in these cities, and the extent to which each of these factors except one influences price. The exact effect of one factor, loss in storage, can not be determined at present, because accurate data on the amount of loss in different years are not available.

[1] *Cf. Infra*, p. 37.

The fundamental factors which influence the price of potatoes to a measurable extent are:

1. Production of potatoes in the entire United States.
2. Loss in storage.
3. Changes in the general price level.
4. A steady and uniform annual increase in the demand for potatoes.
5. Failure of the production of potatoes to increase as rapidly as the demand is increasing.

The following factors which are sometimes thought to exercise a fundamental influence on the price of potatoes have been found to have no measurable effect:

1. Production in the states adjacent to the market (except as it is part of the total United States production).
2. Imports and exports.
3. General business conditions (except to the extent to which they are reflected in the general price level).

A formula has been prepared for use in estimating the price of potatoes in Minneapolis and St. Paul from the available statistics. Ordinarily only two of the five factors influencing price vary much from year to year, namely, production and loss in storage. A third factor, general price level, usually does not change much from one year to the next, tho its fluctuations in recent years have been great. Of the three factors which are the most important of the five, only two can be included in the formula directly, as there are no statistics on losses in storage. Even the production figures are unsatisfactory because inaccuracies in the estimates of changes in acreage of potatoes are so great that it has been found more satisfactory to assume a uniform annual increase instead of using the acreage figures issued by the United States Department of Agriculture.

Despite these limitations, it has been found possible to estimate the average annual price of potatoes in the Twin Cities with an average error of about 9.5 per cent—slightly less than 5 cents a bushel on the basis of the ten-year pre-war average price. Farmers and dealers making use of the formula can remove much of the possibility of error in the estimate by estimating the probable loss in storage and making the necessary allowance in the formula.

DESCRIPTION OF THE MARKET

In order to understand the significance of the various price movements and the forces which cause the movements, it is necessary to know something of the market itself and the way in which it works. The price of potatoes at any time and place is the direct result of the opinions of the men who are buying and selling at that place. To

understand price movements it is necessary to know what factors influence the opinions of these men.

The dealers in Minneapolis and St. Paul may be considered members of a single potato market. These dealers buy from farmers, coöperative associations, or local dealers at country points in the potato producing sections and either ship directly or put the potatoes in storage in their local warehouses. The practice of the Minnesota Potato Exchange differs from the other agencies chiefly in the fact that the Exchange never actually owns the potatoes which it sells. In many respects it may be considered as filling the position of a commission merchant, since the farmers decide when the potatoes shall be sold.

The potatoes which pass through the hands of dealers in Minneapolis and St. Paul are almost entirely sold to wholesalers in cities to the south and east. Roughly speaking, potatoes sold out of the Twin Cities are consumed chiefly in the middle west.[2] Numerous shipments are made into states much farther distant, especially to the south, while occasional cars are sold even in New England and other Atlantic Coast states and in California. Variations in the potato crop in the different sections from year to year cause a wide variation in the amount of potatoes which can be sold in any state. One of the best recognized cases of this sort is that of Iowa. Iowa raises a sufficient acreage of potatoes to supply practically all local needs in a good year, but when the Iowa crop is short, large quantities or Minnesota potatoes are shipped in.

Of course, a large proportion of the potatoes sold from the Twin Cities is intended for seed. Seed stock goes very largely to the southern states, altho there is also a demand for northern seed in middle latitude states. The price of seed stock is determined by forces differing somewhat from those governing the price of eating stock and will be considered only briefly in this bulletin.

CONSIDERATIONS INFLUENCING DEALERS

The question of the factors influencing the price of potatoes in the Twin Cities is best approached by looking at it first from the point of view of the dealer in the Twin Cities. What determines the price for which he will sell potatoes?

First consider a common, but mistaken, answer. It is frequently said that a dealer will be willing to sell for a price that will give him a reasonable margin over what he paid. This is not the case. The good business man will sell potatoes for the best price he can get,

[2] The principal states to which shipments of table stock are made, according to the reports of dealers, are Iowa, Illinois, Kansas, Missouri, Indiana, and Ohio.

irrespective of what he has paid for them. Sometimes it happens
that a dealer makes much more than an ordinary profit on a car of
potatoes, and again it sometimes happens that a dealer loses heavily
on a car of potatoes. The truth is that the price a dealer will pay for
potatoes depends upon what he thinks he can sell them for, always re-
membering, of course, that this is a maximum price; the dealer will
gladly buy the potatoes for less if he can.

In the effort to get the highest possible price, dealers watch the
markets carefully in order to make their sales to the best advantage.
The market news service of the United States Department of Agri-
culture has done much to make it easy for dealers to keep informed
regarding prices and supplies in other markets. Prospective buyers
watch the markets in a similar manner in order to buy to the best
advantage. The result is that prices in all the markets of the country
are very closely related, the price differences being based on the ex-
penses of moving the potatoes along the lines on which it is found
most profitable to move them.
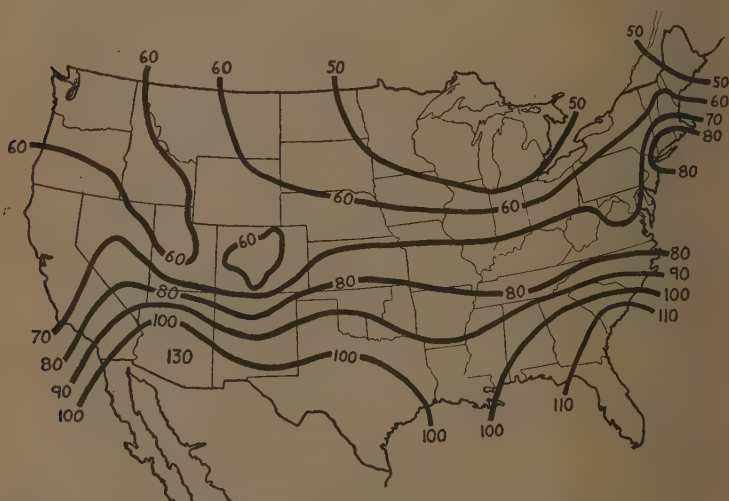
Fig. 1. Isotims (Lines of Equal Price) of Ten-Year Average Farm Price of Potatoes,
December 1, 1906–1915 (cents per bushel)

The map shows clearly the relatively low prices in the surplus-producing regions, increas-
ing in all directions along the lines on which the potatoes are shipped.

The effect of this adjustment is shown in Figure 1, which is an
isotimic map[3] of the average farm price on December 1 for the ten-
year period before the war. The map shows variations in prices from

[3] That is, a map showing lines of equal price. This type of map promises to be quite
useful in showing the geography of prices. The name suggested is from the Greek ἴσος, *equal*,
τιμή, *price*. Strict adherence to the Greek would give the adjective *isotimetic*, but in adapting
it to English use it is better abbreviated to *isotimic*, as the relation to the noun *isotim* is
clearer in this form.

one section to another as an isothermal map shows variations in temperatures. The effect of each surplus-producing region upon the price system is clearly apparent on the map. The largest single surplus-producing area is that including Minnesota, Wisconsin, and Michigan. In these states the price is low, increasing in all directions along the lines the potatoes follow to the regions where they are ultimately consumed. The price system in any one year will usually be quite similar to the one shown on the map, but will vary somewhat from this ten-year average, as the production in certain areas is above or below the average.

TABLE I

TEN-YEAR AVERAGE DECEMBER 1 FARM PRICE OF POTATOES, 1906-15, BY STATES*

State	Price per Bu.	State	Price per Bu.	State	Price per Bu.
	Cents		Cents		Cents
Maine	54	Florida	116	Mississippi	95
New Hampshire..	70	Ohio	64	Louisiana	91
Vermont	60	Indiana	64	Texas	106
Massachusetts ...	80	Illinois	70	Oklahoma	97
Rhode Island....	84	Michigan	45	Arkansas	90
Connecticut	82	Wisconsin	44	Montana	61
New York	63	Minnesota	44	Wyoming	74
New Jersey	76	Iowa	59	Colorado	59
Pennsylvania ...	68	Missouri	74	New Mexico.....	98
Delaware	72	North Dakota ...	52	Arizona	130
Maryland	65	South Dakota ...	54	Utah	59
Virginia	71	Nebraska	64	Nevada	76
West Virginia...	76	Kansas	83	Idaho	51
North Carolina ..	81	Kentucky	76	Washington	56
South Carolina ..	115	Tennessee	77	Oregon	59
Georgia	103	Alabama	98	California	77

* Data from Yearbook of United States Department of Agriculture, 1915, p. 458. These data, together with maps of the production areas and of the railroads of the country, form the basis for drawing the isotims in Figure 1.

The close interrelation of prices all over the United States makes it apparent that the price for which any dealer can sell potatoes depends chiefly on factors over which he individually has no control. Indeed, if dealers did not store potatoes, but merely formed a link in a chain passing the potatoes as rapidly as possible from producer to consumer, dealers would have practically nothing to do with determining the price of potatoes. Price would be determined directly by the willingness of the farmers to sell at the prices consumers were willing to pay.

In actual fact, many dealers are accustomed to store large quantities of potatoes whenever they think they can make money thereby. The dealer who has facilities for storing potatoes considers not only the prices which he can get now for potatoes in the various places where he can sell, but also the prices which he expects to be able to get in the future.

Because of this opportunity to profit by storing, most dealers are always on the alert to judge when prices are "too high" or "to low." If they think prices are lower than is justified by fundamental conditions of demand and supply they buy for storage, expecting prices to rise. Or if they think prices are higher than is justified by fundamental conditions, they work off any stocks they may have on hand and resell every lot as quickly as possible.

The dealer who lays in stocks of potatoes when he thinks prices are too low and sells when he thinks prices are too high and who is skilful enough to judge the market correctly most of the time, is assured good profits. Similarly, the farmer who uses good judgment in deciding when to sell his potatoes will get a better price than will the farmer who uses poor judgment. In fact, it may be laid down as a general rule that everybody engaged in buying and selling potatoes is concerned ultimately with judging what the price "ought" to be— that is, in determining what price is justified by fundamental demand and supply conditions. This is true of dealers, of farmers, and even of some consumers. The only exceptions occur in the cases of those dealers and consumers who make a practice of buying only for immediate needs. Such purchasers keep very small supplies on hand and need to study the market only for the purpose of knowing where to buy to the best advantage, and, perhaps, of postponing purchases a few days at most, in case a temporary shortage develops.

It is apparent, therefore, that the chief force determining the price of potatoes at a particular time is the opinion of buyers and sellers (including chiefly dealers and farmers) as to what price is justified by fundamental conditions of demand and supply. Every farmer and every dealer who plans to lay in stocks of potatoes at favorable times needs to understand these fundamental forces of demand and supply. It is only by understanding them that either farmer or dealer can correctly judge when prices are too low or too high. The remainder of this bulletin is devoted to explaining the operation of the fundamental forces which have been found to be important in determining the price of potatoes in the Twin Cities and to showing how the facts should be interpreted in order to be of use to farmers and to dealers.

BASIS FOR DETERMINING FUNDAMENTAL FACTORS AFFECTING PRICE

Before proceeding further, a word must be said regarding the method by which certain factors have been found to be important in determining prices, and by which the exact effect of each factor has been measured.

Buyers and sellers of potatoes are frequently mistaken as to the price justified by fundamental economic conditions. If such an error

is general in the fall, it may happen, for example, that the price which results is too high. If the price is too high in the early part of the season, potatoes will not be consumed fast enough to dispose of the supply available. Farmers and dealers will then find that not all of the stocks on hand can be sold at existing prices. Since potatoes can not be carried over from one year to the next, the price, under such conditions as have been mentioned, must be lowered enough to permit the supply to be disposed of before the end of the season. A properly adjusted price would remain the same throughout the season, except for a gradual advance to cover cost of storage, and would maintain a fairly uniform consumption throughout the season. But since an abnormally high price early in the season causes small consumption, it must be compensated by an abnormally low price during the remainder of the season, or not all the crop can be sold.

Similarly, if the price is abnormally low early in the season, the supply will be exhausted too rapidly and those who still have potatoes will find that they can get abnormally high prices for them during the remainder of the season. The result is that, altho the price at any one time may differ from the normal price justified by demand-and-supply conditions, the average price for a season will come very close to the normal.

This fact makes it possible to consider the actual average price for a season as the price which was justified by the fundamental demand and supply conditions existing during the season. The price at the beginning of a season is the result of the opinions of buyers and sellers as to what price the fundamental conditions justify. If those opinions are mistaken, the error must be compensated later. The resulting average price may be considered as the effect of actual conditions rather than of mere opinions regarding conditions.

Thus far it has been assumed that a price, for example, 10 per cent too low during the first half of the season, will be compensated accurately by a price 10 per cent too high during the latter half of the season. The curved line in Figure 2, p. 16 (to be explained more fully in a later section), shows the relation between production and price. It may be looked upon also as showing the relation between price and consumption. If the curve be studied from this point of view, it will be seen that a decrease of 10 per cent in the price will increase consumption more than an increase of 10 per cent will diminish it. As a result, it appears that a low price during part of a season will be compensated only by a disproportionally high price during the remainder of the season. The average thus obtained for an entire season will be somewhat higher than the average which would have resulted had a proper price been established at the beginning of the season.

This difficulty is eliminated by taking the harmonic mean of the monthly prices instead of the ordinary arithmetic mean or "average."[4] The harmonic mean is a well recognized type of average used in statistical work. It is equivalent to calculating the average number of bushels sold for a dollar and converting this average into price per bushel. This will not ordinarily give the same result as calculating the average price per bushel in the usual way.

SOURCE OF PRICE STATISTICS

Since the spring of 1917, the local office of the Bureau of Agricultural Economics of the United States Department of Agriculture has been collecting daily information on the price of potatoes in Minneapolis and St. Paul. For the period before the spring of 1917 the only published source of such information is the reports in various daily and weekly papers.

Papers which have to depend upon their own resources to obtain market-price information frequently do not exercise sufficient care in collecting it. Usually they depend upon the opinions of a single dealer, who may be mistaken in his opinion of the ruling price or may even have reasons for somewhat misrepresenting the facts. The task of collecting really accurate information is frequently too difficult and expensive for the ordinary paper to undertake.

Because of the doubtful accuracy of the price data to be obtained from the files of daily and weekly papers, such data have been obtained from the original records of dealers themselves. Four dealers in Minneapolis and St. Paul were found to have records extending as far back as 1912 or earlier. Of these four, three had records going

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[4] If the demand curve were a straight line, a decrease in price would raise consumption by the same amount that an equal increase in price would diminish consumption. The arithmetic average under these conditions would give a price which, if maintained throughout the season, would result in the same consumption as occurred under the varying prices actually existing. The actual demand curve is not a straight line, but if production (or demand) be plotted against the reciprocal of price, the demand curve becomes a straight line. The reciprocals, therefore, may be averaged to obtain the reciprocal of that price which, if maintained throughout the season, would result in the same consumption as occurred under the varying prices actually existing.

The average price just described is the harmonic mean of monthly prices. In using an average, it is always desirable to consider what type of average best describes the important characteristics of the series. In the present instance the average is intended to give a single price which, maintained throughout the season, would be substantially equivalent to the varying price actually observed. The simple arithmetic mean satisfies the condition that the amount paid for the total quantity at that price would equal the total amount paid at the actual prices, assuming an equal amount sold at each price. The harmonic mean satisfies the condition that the amount taken at that price would equal the amount taken at the varying prices actually observed. Obviously the condition satisfied by the harmonic mean is the important requirement for present purposes.

back to 1905 or earlier, and one dealer had records extending back to 1890.[5]

These four dealers made available their original records of car-lot sales, giving the price received for the cars, the freight paid, and, either directly or by calculation, the amount received after the deduction of freight from Minneapolis or St. Paul to destination.

The data obtained began with September, 1899, altho it was later found that nothing prior to September, 1902, could be used in the study, owing to defects in earlier production statistics. Significant prices for Minnesota potatoes could be obtained only for the nine months, September to May, of each year. Very few Minnesota potatoes are shipped in the three summer months.

For the seven seasons, 1899-1900 to 1905-6, records were taken for each business day on which sales were made. Wherever possible, records were taken for three separate car-lot sales on each day. Care was taken to exclude from these records all cars which appeared to contain seed stock, to be in bad condition, or to have any other characteristic which prevented them from being representative sales. Study of actual sales on any day will usually show a large proportion of the sales made at prices which are considerably above or below the going price for average quality table potatoes. The daily prices thus obtained were averaged to obtain weekly, monthly, and annual average prices.

Beginning with September, 1905, records of sales were obtained from three dealers instead of but one, and it appeared sufficient to take records of only three sales each week from each dealer. For simplicity in doing the work, the three records taken each week were for car-lot sales made on the same day, except where three representative sales could not be obtained on the same day. The records thus obtained gave an average price for each month based on either 36 or 45 representative car-lot sales, the exact number depending on the number of weeks in the month. Beginning with February, 1912, similar records were obtained from the fourth dealer, so that for the remainder of the period the average price for each month was based on either 48 or 60 representative car-lot sales.

Beginning with September, 1917, the prices reported by the Bureau of Agricultural Economics, then called the Bureau of Markets, were used. For the four years, 1917-18 to 1920-21, the monthly averages were based on the prices on Tuesday of each week as reported by

the Bureau. For the year 1921-22 the monthly averages were based on the prices of all the business days of each month.

The accuracy of the prices obtained from the dealers for the period after September, 1905, was increased by calculating the average for each dealer for each week, plotting the resulting price curves, and noting all cases where the price of one dealer differed materially from the prices of the others. In every case of discrepancy of this sort the original sales records were examined again without reference to the first set of sales taken off, special effort was made to choose a representative set of sales, and a new price for that week was obtained. In most cases this process resulted in showing that one or two of the sales first taken off for that dealer were not representative.

The weekly prices thus obtained from the separate dealers corresponded very well throughout each year except one, 1910-11. The weekly prices obtained from the separate dealers during 1910-11 showed so little consistency that it seemed better to have more data. Accordingly, a complete new set of prices was obtained for each dealer, for the entire season, taking prices for Fridays instead of for Tuesdays. This second set of prices showed more consistency than the first set, owing to the fact that more sales were made on Fridays than on Tuesdays and it was easier to pick representative sales. Even then there was not as close a correspondence between the weekly prices of the various dealers as existed in the other years. However, when the weekly prices of all the dealers were averaged together in each set separately, the two sets showed substantially the same price movements. Apparently the errors which caused the discrepancies between the prices for individual dealers were chance errors and tended to offset each other when averaged together. This being the case, it was thought best to average together both sets of records obtained for the year. As a result, the prices for 1910-11 are based on twice as many sales as the prices for 1909-10, for example.

In order to determine the accuracy of the methods used, two checks were made. It will be remembered that for the seven years, 1899-1900 to 1905-06, records of sales of one dealer on every business day were taken. Next an entirely independent set of records was taken from the same dealer, using the method adopted for later years, namely, that of taking sales for only one day of each week. The results, shown in Table II, indicate the substantial accuracy of annual averages based on prices of one day each week. Despite the fact that the prices were obtained from but one dealer, the two methods show no discrepancy greater than one cent, and that discrepancy appears in only three out of seven years.

TABLE II

AVERAGE PRICES OBTAINED FROM RECORDS OF DEALER A

Method	Average price for year, per bushel						
	1899-1900	1900-1901	1901-1902	1902-1903	1903-1904	1904-1905	1905-1906
	Cents	Cents	Cents	Cents	Cents	Cents	Cents
Daily records....................	37	35	74	35	72	31	48
Records of one day a week........	36	35	73	36	72	31	48

The second check made was to determine the probable accuracy of the prices obtained for the first six years from a single dealer as compared with the prices obtained during the remaining years from records of several dealers. For this purpose, records were taken of the daily sales of Dealer A during 1905-06 precisely as during the preceding years, and compared with the results obtained by the method followed during the remainder of the period. Table III shows the close similarity between the results of the two methods as applied to the same year.

TABLE III

COMPARISON OF THE MONTHLY AND ANNUAL AVERAGE PRICES PER BUSHEL OBTAINED IN DIFFERENT WAYS FOR THE YEAR 1905-1906

	Daily records	Records from one day each week			
	Dealer A	Dealer A	Dealer B	Dealer C	Average
	Cents	Cents	Cents	Cents	Cents
September	34	35	36	37	36
October	46	45	43	36	41
November	55	56	54	48	53
December	49	49	50	56	52
January	52	51	52	46	50
February	47	47	46	46	46
March	40	40	42	42	41
April	52	53	56	50	53
May	50	52	55	50	52
Average	48	48	48	46	47

Table III shows also the degree of similarity between the results obtained for the several dealers as regards both monthly and annual average prices. It indicates that altho a satisfactory annual average is obtained from a single dealer, taking records of one day each week, the monthly averages so obtained are subject to considerable error. The accuracy of the annual averages obtained from records of one day each week is indicated more completely in Table IV. Only in two years— years of violent price fluctuations—do the annual averages for individual dealers vary more than one or two cents from the average for the group.

At least part of this difference represents an actual difference in the price obtained for the potatoes sold. For example, the potatoes raised in southeastern Minnesota in 1921 were of distinctly poorer quality than

those raised in the Red River Valley region. A dealer handling potatoes chiefly from the southeastern Minnesota region would necessarily obtain a lower price on the average during the 1921-22 season than a dealer handling chiefly Red River Valley potatoes. Similar situations are not uncommon.

TABLE IV

ANNUAL AVERAGE PRICES PER BUSHEL BY DEALERS, 1905-1906 TO 1916-1917

Year		Dealer A	Dealer B	Dealer C	Dealer D	Average	Greatest deviation from average
		Cents	Cents	Cents	Cents	Cents	Cents
1905-06	...	48	48	46	. . .	47	1
1906-07	...	44	43	41	. .	43	2
1907-08	...	55	54	53	. .	54	1
1908-09	...	71	72	72	. .	72	1
1909-10	...	38	35	36	. .	36	2
1910-11	...	57	50	60	. .	55	5
1911-12	...	88	90	87	*	88	2
1912-13	...	39	39	38	40	39	1
1913-14	...	59	61	63	61	61	2
1914-15	...	42	42	†	40	42	2
1915-16	...	67	70	68	71	69	2
1916-17	...	153‡	158‡	155‡	158‡	155‡	3

* Records for four months only were obtained from this dealer for 1911-12.

† Satisfactory prices were unobtainable for certain months. Other months were included in the average for all dealers, however.

‡ The averages are for eight months. So few sales were made in May that representative prices could be obtained from only two dealers, hence the necessity of excluding prices for May in this comparison.

It is commonly supposed that some dealers are able to get better prices, on the average, than other dealers, because of more careful study of the market and favorable trade connections. This is undoubtedly the case to some extent, but the data in Table IV can not be taken as proof of the fact because of the inadequacy of the data. The annual average for each dealer is made up of 38 groups of 3 sales each, the groups being distributed uniformly throughout the season. This is not a large number in view of the difficulty of getting representative sales for each group and of the possibility that all the sales in a single group are occasionally made under abnormal conditions existing for a short time.

Altho the accuracy of the annual averages for the separate dealers can not be trusted to the extent of justifying their use in comparing the ability of different dealers to sell to good advantage, the evidence shown in Table IV indicates their substantial accuracy. The average actual error in the prices for individual dealers is probably not far from one cent. This being the case, the final average price obtained by averaging the prices for all dealers is approximately accurate.

The monthly and annual average prices obtained by the methods described in this section are given in Table VIII at the end of the bulletin. The table gives two figures for each annual average. The

first is the ordinary arithmetic mean of the monthly prices (properly weighted) ; the second is the harmonic mean. The reason for preferring the harmonic mean has already been explained (p. 10).

FUNDAMENTAL FACTORS WHICH DETERMINE PRICE

The important fundamental factors determining the price of potatoes in Minneapolis and St. Paul are:

1. Production of potatoes in the entire United States.
2. Loss in storage.
3. Changes in the general price level.
4. A steady and uniform annual increase in the demand for potatoes.
5. Failure of the production of potatoes to increase as rapidly as the demand is increasing.

Each of these factors requires further consideration.

FACTOR NO. 1.—PRODUCTION OF POTATOES IN THE ENTIRE UNITED STATES

It is obvious that when the production of potatoes in the United States is large, prices must be low, or the potatoes can not be sold. If production were the only factor affecting price, it would be easy to determine the relation between the two. A chart could be made from the statistics of a number of years showing the price which actually accompanied the production which was obtained in each of the years. These points would be found to lie along a smooth curve which could be drawn through them and used as a basis for determining the price which would accompany a crop of any size, within the limits of variation actually observed.

Since several factors in addition to production have an influence on price, the relation between production and price can be determined in practice only by adjusting the actual figures in such a way as to correct for the other factors involved. Figure 2 shows the actual figures for the years 1902-20 with these adjustments made. The factors for whose effect correction is made are: (a) changes in general price level, (b) increase in the demand for potatoes, and (c) failure of the production to increase as rapidly as the demand. Lack of statistics on losses in storage makes it impossible to correct for that important factor. In this chart each dot represents the adjusted price, measured on the vertical scale, which was found to result from the corresponding adjusted production, measured on the horizontal scale.

If correction could be made for losses in storage and if the statistics used were complete and perfectly accurate, the dots in Figure 2
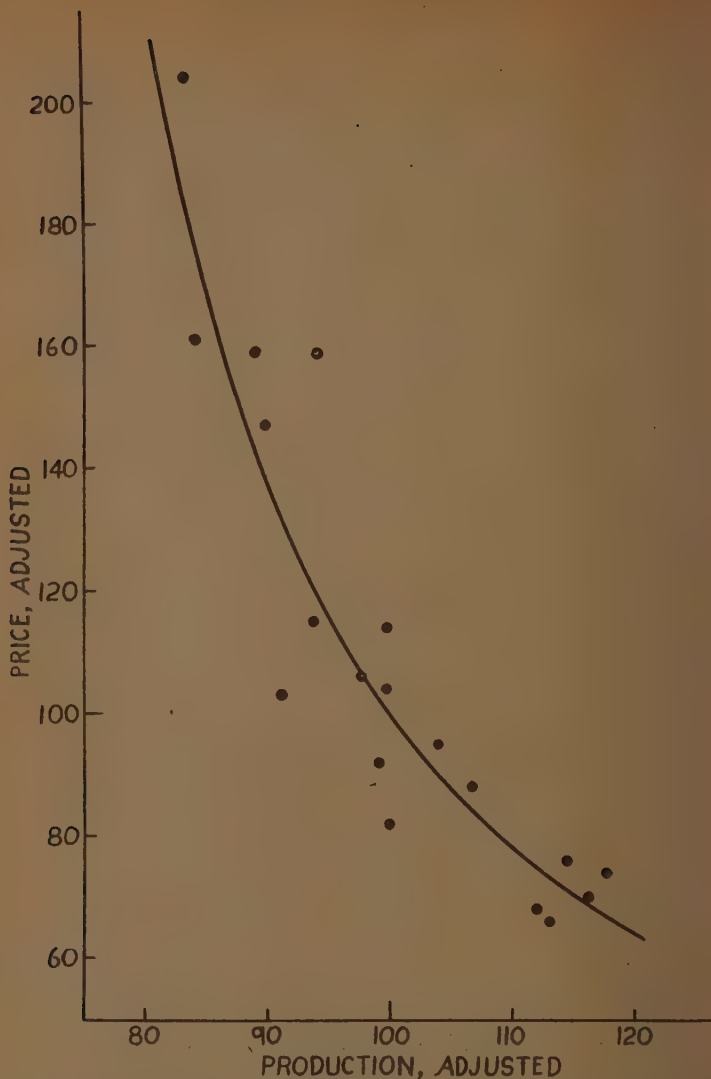
Fig. 2. Relation Between Price and Production

When price and production are adjusted to remove, as far as possible, the effect of other factors influencing the price, the relation between price and production becomes clear. The curve may be looked upon as a demand curve. Its equation is $y = \dfrac{1}{-174.4 + 2.749x}$

would all be very close to a curved line similar to the line shown. In spite of the scattering of the points it is possible by the use of proper mathematical methods[6] to calculate quite accurately the position of the line which the points would approach if the corrections

[6] The method of least squares.

were more nearly complete and accurate.   This is the curved line shown in the chart.

The curved line in Figure 2 may be looked upon as the demand curve for potatoes in the United States, provided certain facts are borne in mind. It shows the amount of potatoes (adjusted) which will be "taken" at each of the various prices (also adjusted) within the range of the curve. By the term "amount of potatoes taken" must be understood not only the amount bought by "consumers" but the amount which will be kept by farmers for their own use and for feeding, and even amounts left in the ground in case the price obtainable does not pay the costs of harvesting. The amounts shown also include the average quantities lost from rotting in storage and in other ways. This differs from the more common interpretation of the demand curve, which attempts to show the "amounts which will be bought" at each of a variety of prices.[7]

The figures for production of potatoes in the United States which are usually accepted are those published by the United States Department of Agriculture. These figures are unsatisfactory because of the tendency for a cumulative error to develop in the estimates of acreage, which are used in arriving at the estimate of total production.   For example, the correction of such an error in the winter of 1921-22 prevented the estimate of production in 1921 from being comparable with the estimate for previous years and caused much difficulty in the potato trade. It has been found more satisfactory in the present study to assume that acreage increases at a perfectly uniform rate, and to neglect the annual estimates of changes in acreage.   The adjusted production data shown in Figure 2 are based on the published estimates of yield per acre applied to an acreage obtained by assuming a uniform annual increase.   Likewise, in the formula for estimating price, which appears farther on in this bulletin, consideration is given to the published estimates of yield per acre but not to the published estimates of acreage.

[7] The concept of the demand curve as describing the amounts taken or kept by everybody in the market, potential sellers as well as potential buyers, seems more useful than the usual concept.   There is excellent support for the concept suggested.   Davenport (*Economics of Enterprise*, p. 51) suggests it when he says: "It is * * * evident that if we decide to regard the money side of the situation as demand for hats, and the hat side of the situation, not as demand for money, but only as supply of hats, we must recognize the holders of hats as themselves having demands for hats."

Wicksteed is strong in his championship of the concept.   Taussig (*Quarterly Journal of Economics*, May, 1921, p. 396) quotes him as follows: "What about the 'supply curve' that usually figures as a determinant of price coördinate with the demand curve?   I say it boldly and baldly: There is no such thing.   What usually figures as such is merely a disguised and therefore unrecognized portion of the 'demand curve.'   Diagrams of intersecting curves (and corresponding tables) of demand prices and supply prices are therefore profoundly misleading. They concentrate the attention of the student upon distinctions which have no theoretical relevancy; they coördinate as two determinants what are really only two arbitrarily and irrelevantly separated portions of one." (*Report of British Association for Advancement of Science*, 1913, p. 568.)

A change in the basis for estimating yield per acre somewhat similar to the recent changes in the basis for estimating acreage gives yield figures since 1902 which are not comparable with the yield figures for earlier years. It is this discrepancy which prevented the inclusion of years prior to 1902 in the statistical study on which this bulletin is based. However, no evidence has been discovered to indicate similar discrepancies in the yield figures for more recent years.

The United States Department of Agriculture is rapidly improving the accuracy of its system of crop estimating. Blame for existing inaccuracy is to be attributed not to incompetency but to lack of sufficient means to accomplish an exceedingly difficult task. It is to be hoped that the methods of crop estimating will soon be sufficiently improved to make the estimates of changes in acreage reliable enough for use in estimating price.

FACTOR NO. 2.—LOSS IN STORAGE

A moment's though leads to the conclusion that loss in storage must necessarily be an important factor affecting price.[8] A loss of 5 per cent of the crop from rot in storage should have approximately, if not precisely, the same effect on price as a decrease of 5 per cent in production.

However, the statement that loss in storage constitutes an important factor affecting price is based upon statistical evidence as well as upon common sense. Mention has already been made of the fact that no accurate statistics are available for losses in storage. However, the heaviest losses in storage result from late blight rot, which is fairly closely correlated with the prevalence of late blight in the field.

Since 1917, the Plant Disease Survey of the United States Department of Agriculture has published estimates of the reduction in yield owing to late blight of potatoes, *Phytophthora infestans*. Since 1919 it has published information also on the prevalence and severity of late blight rot in carload shipments of potatoes inspected by the survey. Estimates of reduction in yield have not been published for earlier years, but the Plant Disease Survey has on record reports from the various states regarding the prevalence of late blight for each year since 1903.[9] Despite the inadequacy of these early reports, it is possible to determine from them whether late blight was light, moderate, or severe in each of the years covered. Column 2 of Table V gives this information.

[8] Throughout the discussion, the term "loss in storage" is used to cover all losses from spoilage, whether occurring in storage, in transit, or even in the bins of retailers or consumers.

[9] The writer is under obligation to Dr. Stakman and Dr. Leach of this station and to the Plant Disease Survey for abstracts of this material.

Figure 2, it will be remembered, shows the adjusted price resulting from the adjusted production of each year, 1902 to 1920. Heavy losses in storage should have the same effect as a decrease in production. Consequently, if we assume that loss in storage is the sole cause of the scattering of the points about the curve, the horizontal distance of each point from the curve should be a measure of the amount of loss in storage. These indications of the amount of loss in storage are shown in column 3 of Table V as light, moderate, or heavy, under the heading "Indicated loss in storage." In connection with the further use of this term, the reader must be careful to bear in mind that the figures for indicated loss in storage are obtained on the assumption that the scattering of the points about the demand curve shown in the chart is caused solely by loss in storage. This is obviously not true, since there is necessarily a certain amount of error in all the statistics used, which accounts for part of the scattering.

TABLE V

CORRELATION OF PREVALENCE OF LATE BLIGHT WITH "INDICATED LOSS IN STORAGE"

Year	Field loss from late blight			Deviation of indicated loss in storage from average loss (per cent of normal production)			Correlation
	Light	Moderate	Severe	Light	Moderate	Severe	
1902-03				−7.7			
1903-04			x			+2.6	+
1904-05		x			+1.0		+
1905-06			x	−7.5			−
1906-07	x				+1.7		
1907-08	x					+4.2	−
1908-09	x				+1.6		
1909-10	x			−4.7			+
1910-11	x				0.0		
1911-12	x				−1.8		
1912-13		x				+5.3	
1913-14	x				−1.3		
1914-15		x				+3.0	
1915-16			x		+1.2		
1916-17	x				+2.0		
1917-18		x			+2.3		+
1918-19	x			−4.0			+
1919-20			x			+7.5	+
1920-21			x	−4.8			−

Column 4 of Table V shows the correlation between the extent of late blight in the fields and the indicated loss in storage, a plus sign indicating definite correspondence, a minus sign indicating definite lack of correspondence, and no sign being shown where the correspondence or lack of correspondence is not definite. For example, when a moderate indicated loss in storage is associated with either light or severe occurrences of late blight, or vice versa, there is no definite indication of either correspondence or lack of correspondence because of the

rough character of the classifications. The nature of the data on prevalence of late blight renders more refined calculation impossible.

Table V shows that out of nine years for which the facts are definite enough to form a basis for conclusions there were six in which the indicated loss in storage corresponded with the prevalence of late blight and three years in which the two failed to correspond. This is probably as close a correspondence as could be expected, even on the assumption that the "indicated loss in storage" is identical with the actual loss in storage. Considerable loss in storage is due to blackleg rot, *Fusarium,* and the potato leak, in addition to late blight rot. Furthermore, losses in storage from late blight rot are only roughly proportional to the prevalence of late blight. Some indication of this is given in figures published by the Plant Disease Survey. The estimated reduction in yield due to late blight was almost twice as great in 1920 as in 1919, the figures being 4.7 per cent for 1919 and 7.9 per cent for 1920. However, losses from late blight rot in storage appear to have been much more severe in 1919 than in 1920. The Plant Disease Survey reports that in 1919, 5959 cars were inspected, of which 1000 had late blight rot present, with an average percentage of rot, when present, 8.3. In 1920, 5140 cars were inspected, of which 651 had late blight rot present, with an average percentage of rot, when present, of 5.6.

In the presence of so many disturbing factors, close correspondence between prevalence of late blight and total losses in storage from all causes is not to be expected. The existence of such correlation as is found between prevalence of late blight and indicated loss in storage may be taken as evidence that the indicated loss in storage is close to the actual loss in storage, in other words, that loss in storage is the only important factor not allowed for in the adjustment of production and price for Figure 2.

More conclusive evidence as to whether loss in storage is the only important factor not corrected for may be obtained by judging whether actual variations of loss in storage might reasonably be almost as great as the variations of indicated loss in storage. The average of the three years of least indicated loss in storage is less than the average loss by 6.3 per cent of the normal production. The average of the three years of greatest indicated loss in storage is greater than the average loss by 5.7 per cent of the normal production. This represents a range between the three years of lowest indicated loss and the three years of highest indicated loss of 12 per cent of the normal production.

It is difficult to get any figures on actual loss in storage, but estimates have been obtained from a number of growers and dealers and others interested in such losses. These estimates place the average

loss in storage for the entire United States at from 10 to 15 per cent of the crop. The variation to be frequently expected in this loss is estimated at from 3.5 to 5 per cent above and below the average. According to these estimates, the range to be expected is from 7 to 10 per cent. If these estimates are approximately correct, there remains only about half of the indicated loss in storage to be explained by inaccuracies in the data and other factors.

The figures for "indicated loss in storage," it will be remembered, are based on the discrepancy between the actual price and the estimated price, on the assumption that loss in storage explains all of that discrepancy. However, it is necessary to assume considerable inaccuracy in the data used. The production estimates used included no correction for changes in acreage other than a uniform annual increase; the yield figures are subject to a certain degree of error, the amount of which can not be determined; the wholesale price index number does not give an entirely accurate measure of the changes in the general price level; the annual increase in the demand for potatoes, and the extent to which production is lagging behind this increase, may have been measured somewhat inaccurately; even the figures on the price of potatoes are subject to some error. All of these inaccuracies result in increasing the variation in the indicated loss in storage. This may easily account for the variation which is not accounted for by variation in actual loss in storage.

Any other factor affecting price would have an effect similar to that of loss in storage in increasing the variation in indicated loss in storage. With 7 to 10 per cent of this variation accounted for by actual loss in storage and most of the remaining variation accounted for by inaccuracies in the data used, there is no room for supposing that there are any important factors affecting price which have not been considered. Any factors in addition to the five important ones herein discussed must have a very minor effect on the price of potatoes.

The demonstration of the importance of loss in storage as a factor affecting price indicates the necessity for compilation of statistics on these losses. Collection of such figures is of even greater importance than improvement in the accuracy of the estimates of acreage and yield. Investigations should also be made to devise methods of forecasting loss in storage. Losses from such causes as late blight rot and *Fusarium*, which are dependent upon field infection, should offer opportunity for fairly accurate prediction before the crop is harvested. Statistical studies of the effect of weather conditions upon infection and development of rots should yield valuable results in making possible the forecasting of losses from weather conditions in the late summer and fall.

FACTOR NO. 3.—CHANGES IN THE GENERAL PRICE LEVEL

Changes in the general price level in the United States are best measured by the Bureau of Labor Statistics "all commodities" index number of wholesale prices. Changes in the general price level are not really causes of changes in the price of potatoes; both are the results of other causes. However, too little is known as yet regarding the causes of changes in the general price level to make it profitable to consider directly the effect of these causes on the price of potatoes. It is much more satisfactory to consider the relation between their effect on the price of potatoes and their effect on the general price level.

For convenience, the changes in the general price level may be divided into three classes: (1) General long-time tendencies; (2) large and violent fluctuations covering a relatively short period of years (the recent war-time inflation); and (3) the moderate fluctuations which recur with each cycle of business prosperity and depression. The price of potatoes has shown a general trend somewhat different from that of the general price level, owing to the failure of the production of potatoes to increase as rapidly as the demand, a factor to be discussed in detail later. Aside from this difference in general trend, the price of potatoes has been found to be subject apparently to the same influences as the general price level and to be affected by them in the same degree. Correction being made for those factors which affect the price of potatoes, but do not appreciably affect the general price level, the price of potatoes appears to move in exact unison with the general price level.[10]

[10] This statement is based, (1) on the fact that by estimating price on this assumption, as accurate estimates are obtained for the recent years of violent price fluctuation as for earlier years; (2) on negative results obtained in a multiple correlation study using yield per acre, price corrected for changes in the general price level, and the Harvard Price Index of Business Cycles; and (3) on correlations of month-to-month changes in the price of potatoes with month-to-month changes in "all commodities," "food," and "farm products" index numbers of the Bureau of Labor Statistics. The latter correlations give the following results:

Index number	Coefficients of correlation of month-to-month changes, price preceding (—) and following (+) the index number							
	1900-1915				1915-1921			
	−2 mo.	−1 mo.	0 mo.	+1 mo.	−2 mo.	−1 mo.	0 mo.	+1 mo.
All commodities	+0.09	+0.31	+0.21	+0.04	.....	.....	+0.51	.....
Food	−0.01	+0.32	+0.19	.....	.....	+0.34	+0.65	.....
Farm products	+0.14	+0.38	+0.21	+0.01	.....	+0.20	+0.38	.....

Except for the small coefficients, the probable errors are all relatively very small.

FACTOR NO. 4.—A STEADY AND UNIFORM ANNUAL INCREASE IN THE DEMAND FOR POTATOES

It is unnecessary to determine the amount of the annual increase in demand since the effect of the increase is taken care of in an indirect manner by the method used for expressing changes in production and by the determination of the effect of failure of production to increase as rapidly as demand is increasing. The fact that the demand for potatoes in the United States is increasing is obvious and requires no discussion here. The conclusion that the increase is by uniform annual amounts is based on the fact that the general trend of production is satisfactorily indicated by a straight line and the further fact that the measure of the failure of production to increase as rapidly as the demand is increasing is also a straight line. It follows that, within the limits of accuracy fixed by the character of the data, demand is shown to be increasing by uniform annual amounts.

FACTOR NO. 5.—FAILURE OF THE PRODUCTION OF POTATOES TO INCREASE AS RAPIDLY AS THE DEMAND IS INCREASING

The conclusion that the production of potatoes is increasing less rapidly than the demand follows from the fact that the price of potatoes is rising relative to the general price level. This may be seen from a chart showing the changes in the price of potatoes and also the changes in the general price level. It appears more clearly on a chart showing the relative price of potatoes, calculated by dividing the price of potatoes for each year by the corresponding value of the index number of whole-sale prices.

The steady increase in the price of potatoes relative to the general price level is practically identical with the increase which has taken

The regression coefficients are also important:

Index number	Regression coefficients of price on index number for month-to-month changes, price preceding (—) and following (+) the index number							
	1900-1915				1915-1921			
	—2 mo.	—1 mo.	0 mo.	—1 mo.	—2 mo.	—1 mo.	0 mo.	—1 mo.
All commodities ..	+9.79	+0.89	+1.67	+0.12	.....	.....	+1.81	.....
Food	—0.37	+1.55	+0.82	.....	.....	+0.90	+1.71	.....
Farm products ..	+0.48	+2.91	+0.70	+0.04	.....	+0.68	+1.10	.....

For the entire period, the price of potatoes in cents averaged from 0.61 to 0.64 of the value of the various index numbers. Accordingly, if the price of potatoes were affected in the same degree as the index number by the forces which caused changes in the index number, a change of one cent in the price of potatoes should accompany a change of 1.64 to 1.56 in the index number. The regression coefficients of price on the "all commodities" index number are fairly close to these figures for the lags which show the best correlations. The same is true for the regression of price on the "food" index number, but not for the regression of price on the "farm products" index number.

place in the price of almost all farm products. The chief cause appears
to be the fact that it is no longer possible to increase production by set-
tling new areas of highly productive farm land. Production may now
be increased only by obtaining higher yields per acre or by making use
of poorer land. Either method involves increased expense of pro-
duction. Under these conditions, production can continue to increase
only in response to higher prices for the product. The potato crop is
only one of many farm products which are feeling the effect of the
same forces.[11]

FACTORS WHICH DO NOT INFLUENCE PRICE TO A MEASURABLE EXTENT

The following factors have been studied with care to determine
whether they should be considered in estimating price. As far as can be
determined from a study of the data for 19 years, these factors have no
measurable effect on the price of potatoes in Minneapolis and St. Paul.

1.—PRODUCTION IN THE STATES ADJACENT TO THE MARKET

The production of potatoes in the states nearest Minneapolis and
St. Paul constitutes part of the total production of the United States.
To that extent, the effect of variations in the production in these states
is allowed for when total United States production is considered in
estimating the price of potatoes. However, it is commonly thought that
variations in production in the region surrounding Minneapolis and
St. Paul have a much larger effect on price in those cities than similar
variations in production in Maine or even in Michigan. It is natural
to suppose that in any two years in which the production in the entire
United States is normal, but in which the production in Minnesota

[11] This discussion contains an implication which will meet with objection from some
economists. It assumes that if supply remained constant, an increase in price which exactly
equaled the increase in the general price level would indicate a constant demand; in other
words, that the taking of the same quantity of a commodity at a higher money price does not
in this case signify an increased demand. This immediately raises the weighty objection that
demand is to be measured in terms of quantities taken at particular money prices. An illustra-
tion of the force of this contention appears in the fact that changes in general price level
occur only through changes in prices of individual commodities and must be studied as results
of changes in the demand for those commodities.

On the other hand, there is much occasion for discussing demand in terms of purchasing
power offered for various quantities of a commodity rather than in terms of the number of
coins offered. The present case is such an instance. The confusion arises from the difficulty
of adapting to the actual facts the terms and concepts worked out for a theoretical analysis
under the assumptions of *caeteris paribus*.

It appears to the writer that where important changes in the purchasing power of money
are involved, the concepts of the usual demand and supply analysis are more accurately fol-
lowed by expressing demand in terms of purchasing power rather than in terms of money.
However that may be, the term "demand" must continue to bear the burden of a multitude of
meanings, to be much abused and be the source of many misunderstandings, until some general
agreement fixes upon other terms to carry some of the various meanings now forced on one
word. The usage here adopted has abundant support and, for the present at least, seems to
offer the best means of expressing the facts.

varies widely, different prices in Minneapolis and St. Paul will result; that the effect of an excess production in Maine will not offset the effect of an equal deficiency of production in Minnesota, as far as the local price is concerned.

An investigation was made to determine the effect of variations in the production of Minnesota and Wisconsin taken together on the price of potatoes in Minneapolis and St. Paul. This investigation resulted in the discovery that variations in the production in Minnesota and Wisconsin had no measurable effect on the price of potatoes except to the extent that the production for the entire United States was affected.

Altho the fact is surprising, it is very readily explained when once recognized. The explanation will be somewhat clearer if the price situation as shown in Figure 1, p. 6, is borne in mind. Consider the extreme case of an excess production in Minnesota exactly equaled by a deficiency of production in Maine. In order to take care of the deficiency in the supply for New York City, for example, an unusual quantity is shipped in from New York and Pennsylvania. Large quantities of potatoes having been shipped east instead of west from New York and Pennsylvania, their place is taken by Michigan potatoes. But since Michigan potatoes are being shipped somewhat farther east than usual, Minnesota potatoes can be sold without competition in what is ordinarily Michigan territory. The result is that the Minnesota potatoes sell at practically the same price that would have been obtained if production in both Minnesota and Maine had been normal.

2.—IMPORTS AND EXPORTS

Altho the statistical study showed no measurable effect of imports and exports on price, the results should be interpreted as indicating that such effect as they have is very small. The effect may be assumed equal to that of a corresponding increase or decrease in the total United States production.

The effect of imports and exports on the price of potatoes has been studied both directly and indirectly. Direct study by a multiple correlation of price, net imports, and yield, gave negative results. Since imports and exports are likely to be very incompletely reported whenever there is no duty to be levied, an indirect method was tried also. This method was based on the fact that most of our imports come from Canada. Comparison of the relative size of the Canadian and United States production for each year offers a basis for judging the probable importance of imports from Canada. However, there was no evidence that variation in the Canadian crop had any measurable effect on the price of potatoes in Minneapolis and St. Paul.

The explanation of the failure to discover any relation between imports and exports and price is probably to be found in the relatively

small amounts imported and exported. The largest net importation in recent years was that of 1911-12, amounting to about 12,500,000 bushels. This was only 2.3 per cent of the United States production. The largest net exportation was in 1915-16 and amounted to about 3,800,000 bushels, or 0.9 per cent of the United States production. The heavy imports of 1911-12 came chiefly from the United Kingdom, imports from that source amounting to about 12,600,000 bushels. Since that year, quarantine regulations have excluded importations from all important sources except Canada and Bermuda. The largest net importations since 1911-12 were in 1919-20 and amounted to about 3,200,000 bushels, or 1.1 per cent of the United States production. Since these are extreme figures, it is apparent that imports and exports should not be expected to have any important effect on price.

3.—GENERAL BUSINESS CONDITIONS

The general price level is affected by business conditions, rising in periods of prosperity and falling in periods of business depression. However, the prices of some commodities are affected by these conditions much more than the general price level. Professor Persons has constructed a "Commodity Price Index of Business Cycles"[12] for which the fluctuations in each of the business cycles from 1900 to 1915 are about three times as great as those of the Bureau of Labor Statistics index number of "all commodities." Six of the ten commodities included in this index number are of agricultural origin, namely, hides, cotton sheetings, print cloths, worsted yarns, salt mess pork, and cottonseed oil. It appeared possible that potatoes might be similarly affected.

On the other hand, it appeared possible that potatoes, being a relatively cheap food, might be in greater demand during periods of business depression and less used in periods of business prosperity. If such were the case, potatoes would rise in price when most other commodities fall, and fall when most other commodities rise. It is certain that many commodities remain relatively unaffected by the business cycle or possibly even fall in price in periods of prosperity.

The possibilities suggested above made necessary a very careful study of the relation between the price of potatoes and the business cycle. The results obtained indicated that the influences connected with the business cycle affect the price of potatoes to the same degree that they affect the Bureau of Labor Statistics index number of "all commodities." This conclusion has been discussed already at greater length on page 22.

[12] *Cf. Review of Economic Statistics,* Nov. 1921.

USE OF THE PRICE–ESTIMATING FORMULA
ESTIMATION OF AVERAGE PRICE FOR THE SEASON

In order to estimate the price justified at any particular time by fundamental conditions of demand and supply, it is necessary first to estimate the average price for the season. Statistical study of the price of potatoes for the years 1902-3 to 1920-21 gives the following formula for estimating the average price in Minneapolis and St. Paul for the season September 1 to May 31:

$$\text{Price per bushel} = \frac{L \times T}{2.83Y - 174} \qquad (1)$$

- Market price is now ordinarily quoted in terms of hundredweights, for calculation of which the following formula is used instead of the one just given:

$$\text{Price per hundredweight} = \frac{L \times T}{1.70Y - 105} \qquad (2)$$

Figures to be used in place of the letters in these formulas are obtained as follows:

L—Price level. The Bureau of Labor Statistics "all commodities" index number, 1913 = 100, must be used and an estimate made of its probable average for the nine months, September to May.

Y—Average yield per acre for the United States as a whole, from estimates of United States Department of Agriculture.

T—Values for this quantity for the years 1921-22 to 1924-25 are given in Table VI. The quantities shown are obtained on the assumption that the increase in demand for potatoes and the failure of production to increase as rapidly as demand continue as in the past. The values are shown for but a short period of years because they are better recalculated every few years.

TABLE VI
VALUES OF T

Year	T
1921-22	57.6
1922-23	62.9
1923-24	69.4
1924-25	77.3

These formulas for estimating price take care of the effect of changes in production, of changes in the general price level, of the increase in demand for potatoes, and of the failure of production to increase as rapidly as demand is increasing. The only important factor not included is loss in storage. However, any one who is able to arrive at an estimate of the amount of loss in storage in which he

feels confidence can readily include its effect in the formula, as will be explained later. Most dealers, at least, will wish to make this correction.

It will be noted also that no account is taken of estimates of acreage. As a matter of fact, the formulas allow for the normal average annual increase, but for no other changes in acreage. It would be very easy to make allowance for changes in acreage if sufficiently accurate estimates of these changes could be obtained. The best estimates obtainable—those of the United States Department of Agriculture—have been subject to enough error to destroy entirely their value for use in preparing an estimate of price. The extent of the errors in the original estimates is indicated by the revisions which have been necessary, as shown in Figure 3. It is doubtful whether the year-to-year changes in even the revised figures are very reliable.
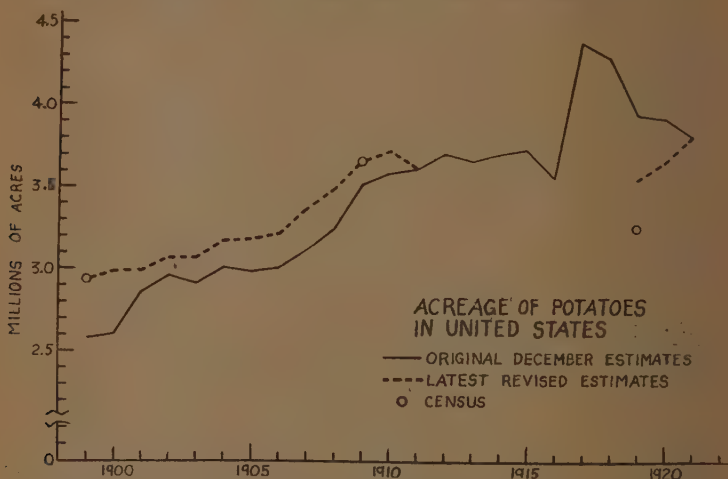
Fig. 3. Acreage of Potatoes in United States

The inaccuracy of the original estimates of acreage of potatoes shows why the acreage figures are of no value in estimating price. It is to be hoped that improved methods of crop estimating which are being adopted will soon result in estimates accurate enough to be of more value.

The Department of Agriculture is making great improvements in the accuracy of its crop estimates and it is possible that estimates of acreage are already sufficiently accurate to be of use in estimating price. Further study is necessary to find out whether this is the case. In the meantime, farmers and dealers should use their influence to bring about more adequate support for the important work of the crop-estimating service of the Department of Agriculture. No forecast of

prices can be more accurate than the figures on which it is based. Potato growers and potato dealers are in serious need, not only of more accurate estimates of acreage, but also of data on losses in storage and in transit and of early estimates of probable losses. It is also probable that the estimates of yield can be considerably improved. especially the early estimates based on condition reports. So far as is known, the Department of Agriculture has made no use of the method of predicting yields from weather conditions. Professor H. L. Moore has shown that estimates of the probable yield of cotton made from weather conditions are considerably more accurate than the Department's estimates based on reports of condition of the crop.[13] In view of the importance of its work, the crop reporting service of the Department of Agriculture deserves more liberal support.

Altho no estimates of probable loss in storage are now available and much work will probably be required before accurate estimates can be made, some idea of the probable loss can be obtained from reports on the prevalence of late blight and of *Fusarium*. Such reports are now published by the Plant Disease Survey of the United State Department of Agriculture. Any one who feels some confidence in his ability to estimate loss in storage can readily make use of such estimates in forecasting price.

In order to make allowance for loss in storage in the price-estimating formula, it is necessary merely to estimate the percentage of the crop over or under the average which will be lost in storage and correct the yield figure accordingly. The formula makes allowance for average loss in storage. If it is estimated, for example, that 5 per cent more of the crop will be lost in storage than is lost on the average, the yield figures used in the formula should be reduced 5 per cent from the estimated actual yield. Potatoes lost in storage have no more ultimate effect on price than if they had not been raised. Similarly, if it is estimated that 5 per cent less of the crop will be lost in storage than is lost on the average, the estimated yield should be increased 5 per cent for use in the formula. As has been said, the formula provides for average loss in storage.

The relative completeness with which the factors included in the formulas determine price is indicated in Figure 4. The average error is 9.5 per cent. In calculating the estimated price for each year, the yield figures of the Department of Agriculture are used directly, with no correction for probable loss in storage. As shown in Table V, p. 19, the discrepancy between the actual price and the estimated price in 1919, the largest discrepancy found, would be completely explained if 7.5 per cent more of the crop were lost in storage than is lost on

[13] *Cf.* H. L. Moore, *Forecasting the Yield and the Price of Cotton.*

the average.   More than half of the discrepancy would be explained
by a loss in storage only 4 per cent higher than the average.
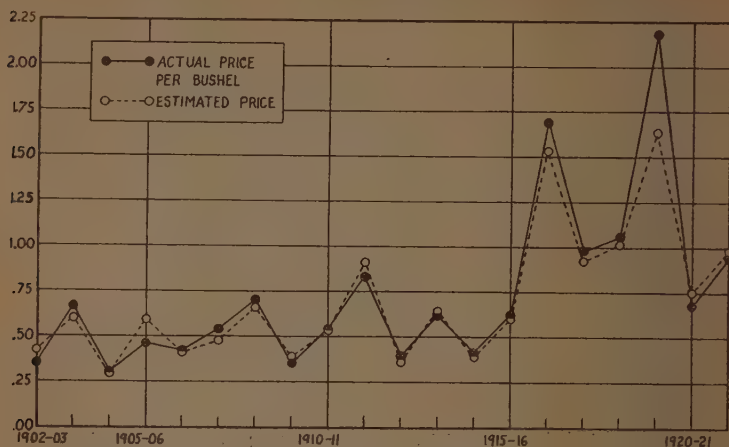
Fig. 4. Actual and Estimated Prices of Potatoes, 1902-03 to 1920-21

The estimated prices are obtained by means of the formulas presented in this bulletin.
No correction was made for loss in storage in any of the estimates shown.   The difference be-
tween the actual price and the estimated price should usually be judged in terms of percentage
rather than in terms of actual amounts.   The average error is 9.5 per cent.

The difference each year between the calculated price and the ac-
tual price is to be attributed to the following causes which are put into
groups according to their relative importance:

1. Loss in storage.   This factor is probably about as important
   as all the rest taken together.

2. (a) Errors in the actual price shown.   The price estimate is
   for "average quality table potatoes."   The average qual-
   ity of the potatoes actually sold varies considerably from
   year to year, so that the price given is not an accurate
   indication of the price for "average quality table potatoes."

   (b) Changes in acreage which can not be considered because
   of the inaccuracy of the estimates.

   (c) Errors in the yield estimates.

   (d) Inaccuracy in the index number of general price level.

3. (a) Inaccuracy in the calculated values used in the formula.
   Every effort has been made to obtain accurate values, but
   it is probable that there is some error in the values
   obtained.

   (b) The factors found to have "no measurable effect" prob-
   ably have some actual effect on price.   There are probably
   other factors of minor importance which might have been

considered. If all these factors should act in the same
direction in any year, the effect would be appreciable.

(c) The actual price for the season is not always the price
which should have resulted from the fundamental demand
and supply conditions. A striking example appears in
1917-18. The price was so high during most of the season
that a large amount of old crop potatoes was held over
into the summer.

ESTIMATION OF AVERAGE PRICE FOR A MONTH

The price which fundamental conditions of demand and supply
justify as an average for the season is not justified for each month of
the season. Any one planning to hold or store potatoes until later in
the season must receive a considerably higher price for the potatoes
in the later months because of the expenses of storing and especially
because of the shrinkage caused by rotting and by loss of weight from
evaporation of moisture. In order to encourage the necessary storing
of potatoes, the price must average considerably higher in the spring
than in the fall. Costs of storing, including shrinkage, vary widely
with different individuals and in different years. The most satisfactory
way of determining the necessary seasonal variation in price is from
the average variation in past years. Table VII and Figures 5 and 6
show the normal seasonal variation so determined.

TABLE VII

SEASONAL VARIATION OF PRICE OF POTATOES IN MINNEAPOLIS AND ST. PAUL
(16-YEAR AVERAGE, SEPTEMBER, 1899 TO MAY, 1915)

Month	Average price	Per cent of average for season
	Cents per Bu.	
September	49.4	96.2
October	45.5	88.6
November	47.1	91.7
December	47.9	93.2
January	51.5	100.3
February	54.8	106.6
March	55.6	108.3
April	57.1	111.1
May	56.4	109.9
Average (Harmonic mean)	51.36	100.0

To calculate the price of potatoes which appears justified for any
month, it is necessary merely to multiply the calculated average for the
season by the appropriate percentage as given in column 3 of Table VII.
This gives the market price to be expected, based on the figures on
fundamental conditions which were used in calculating the average
price for the season.
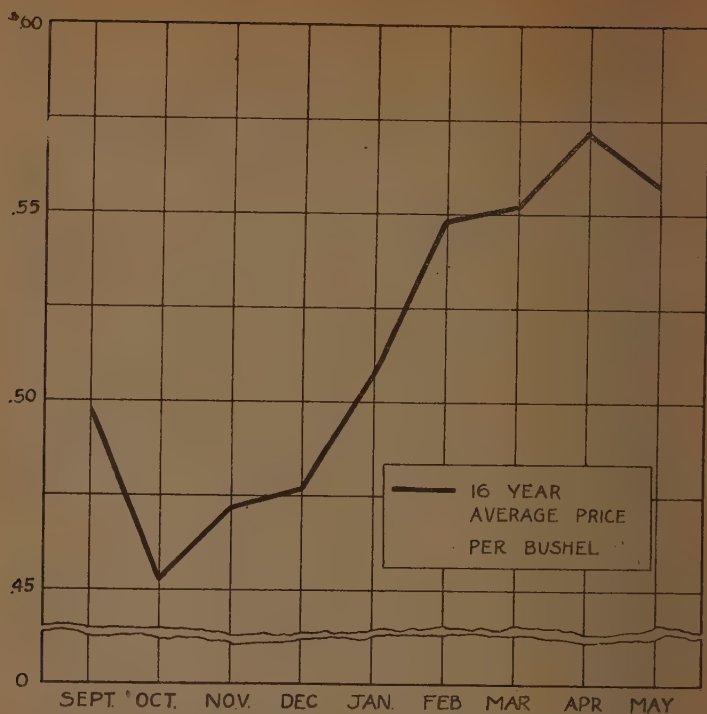
Fig. 5.   Average Monthly Price of Potatoes for Sixteen Years

The price of potatoes in Minneapolis and St. Paul averages much higher in the spring than in the fall. This increase is necessary to compensate for shrinkage of potatoes in storage and for the cost of storage.

Figures 7a and 7b show the actual price of potatoes in Minneapolis and St. Paul monthly and also the price estimated by the methods which have been described.[14]   The "first estimated price" is based on the average of the Bureau of Labor Statistics wholesale price index number for nine months, and therefore assumes that changes in the general price level for the entire season could be foreseen.   The "second estimated price" bases the estimate for each month on the actual index number for that month.   In ordinary years the two estimates give practically identical results, but under conditions such as existed during the war, it pays to try to look ahead.

A farmer who is considering holding his potatoes or a dealer who is considering buying for storage may use these monthly estimates in

[14] These charts were made on the basis of a formula calculated before the advantage of using the harmonic mean was discovered.   As a result, the differences between the actual prices and the estimated prices here shown are not the same as appear in Figure 4.   They also differ in that Figures 7a and 7b are "ratio charts"—a given vertical distance represents the same *percentage* difference in all parts of the chart.   The conclusions to be drawn from these charts are not affected by the slight error in the formula used.

either of two ways. (a) He may calculate the price which appears to be justified at that particular time and base his action on the difference between the actual price and the estimated price. (b) He may calculate the estimated price for the month when he expects to sell and see if the difference between that estimated price and the actual price at the time will give him a profit over the cost of storage. Any one, whether farmer or dealer, who plans to use the estimates in either of these ways should read the last section of this bulletin, "Suggestions for a Selling Policy for Farmers." Most of the suggestions apply to dealers as well as to farmers.
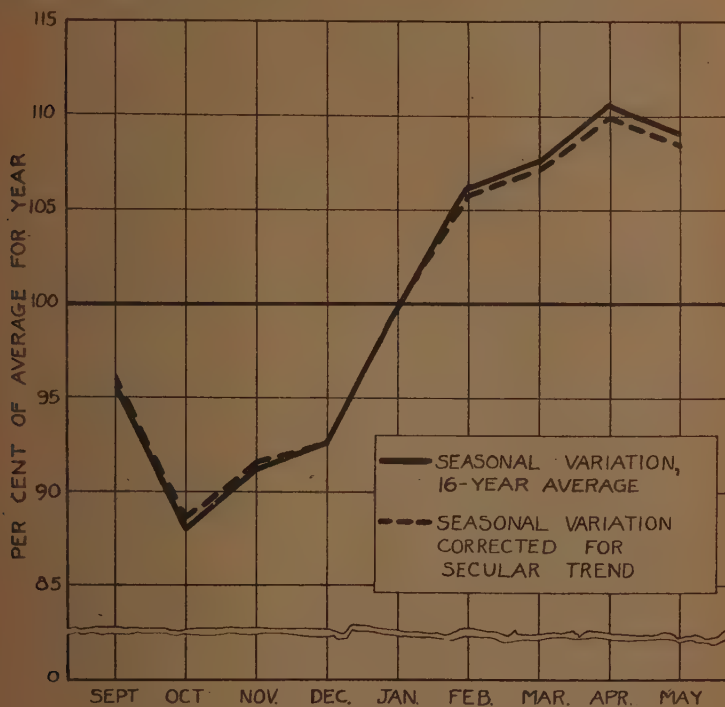
Fig. 6. Seasonal Variation in Price of Potatoes

Variation in price of potatoes during the season is shown here in terms of percentage, the average for the year.

CORRECTION OF ESTIMATE FOR QUALITY OF POTATOES AND FOR OTHER MARKETS

In using the formula for estimating price, it is necessary to keep in mind exactly what the estimate is. The formula uses estimates of fundamental demand and supply conditions to calculate a price which applies only to *average quality table potatoes on the wholesale market*
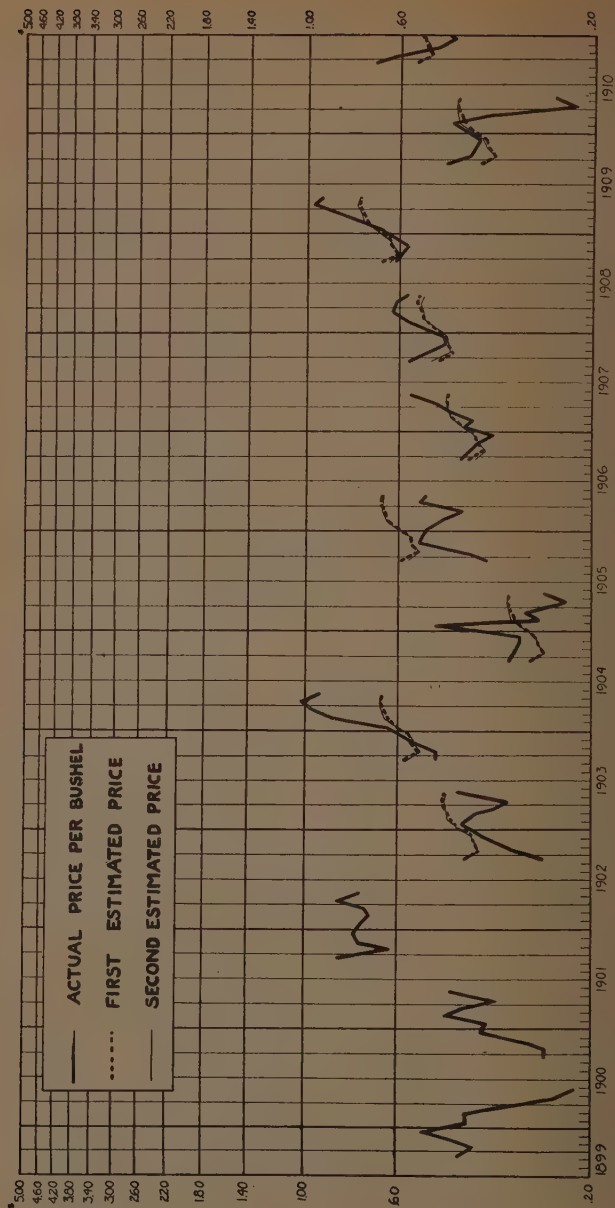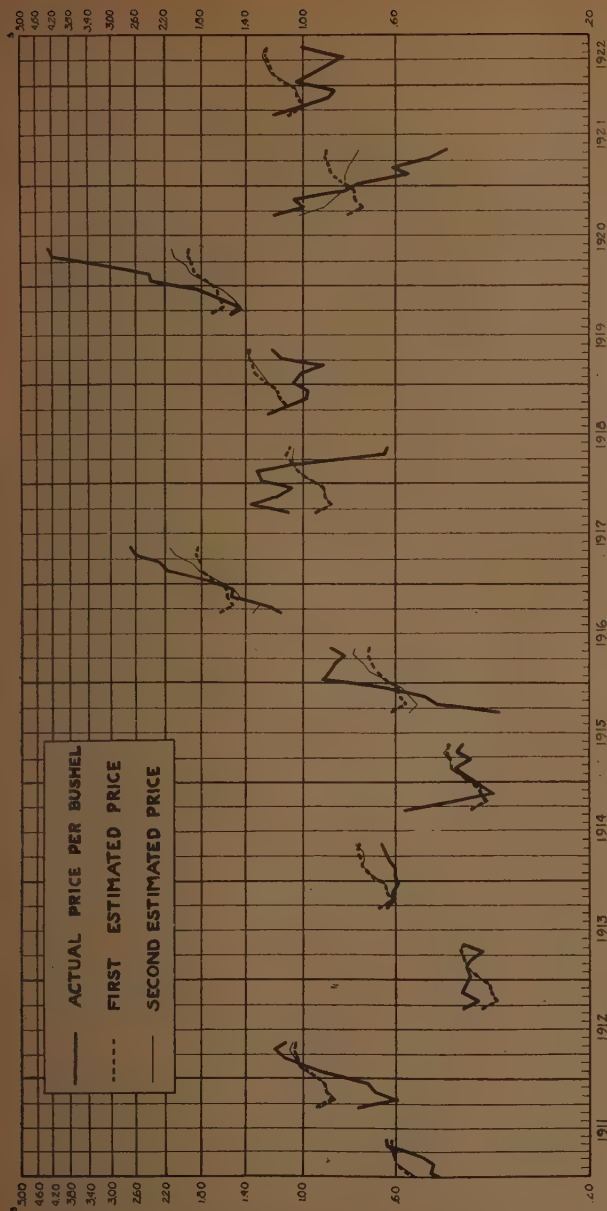
Fig. 7. Actual and Estimated Prices of Potatoes Monthly, 1899-1921

Monthly estimates of prices may be based either on the average price level for the season (first estimate) or on the price level for each month separately (second estimate). Usually the two are almost identical, but in 1920-21 it would have paid to look ahead in order to try to use the first estimate, which indicated that the actual price in the fall was much too high. This is a "ratio chart," that is, a given vertical distance represents the same percentage difference in all parts of the chart.

of Minneapolis and St. Paul. The result obtained may be corrected, however, to apply to distant markets and to various qualities of potatoes.

The necessity of correcting the estimated price of potatoes for differences in quality is obvious and needs little discussion. It should always be remembered that quality of potatoes is not to be judged by personal preferences but by market requirements, which are determined by the preferences of consumers. Uniformity and careful grading are important factors in obtaining good prices.

The price of potatoes in other localities may be estimated by calculating the price for Minneapolis and St. Paul and adding or subtracting the normal difference between the price in those cities and the price in the place for which the estimate is being made. Calculating the price in this way does not necessarily imply that the Twin City market fixes the price for other localities. The price-estimating formula takes into consideration only the fundamental forces which fix the price of potatoes over the entire United States. It measures the effect of these forces as applied specifically to the price in Minneapolis and St. Paul. As indicated in an earlier discussion,[15] prices in the various parts of the United States are closely related, the differences being the costs of moving the potatoes. Consequently, the forces which fix a certain price in Minneapolis and St. Paul will fix prices elsewhere which will differ by no more than the costs of moving the potatoes. In calculating these costs, however, it is frequently necessary to allow much more than freight charges. If several dealers must handle the potatoes, their margins must be added to the costs of moving the potatoes.

Farmers may correct the estimated prices to apply to their local market in exactly the same way that they correct the current quotations of actual prices. The only difference is that the actual prices are affected slightly by variations in the quality of the potatoes on the market, while the estimate always applies to potatoes of "average quality." In connection with both the estimated price and the quotations it should be remembered that they are based on the price of potatoes sold delivered to the buyer, less freight charges. In cold weather the dealer has additional expenses for heater service or else takes a chance of loss from freezing, and usually takes a larger margin to cover the added expense or risk.

Prices calculated by the formula may also be corrected to apply to Chicago, Kansas City, St. Louis, and even more distant markets by merely adding the proper market differential. Price so calculated may be considered quite accurate. It is highly desirable, however, that

[15] *Cf. supra* pp. 6 and 7.

similar formulas be worked out for all important markets. This would give an opportunity for checking results: for example, Twin City dealers could check the estimate given by the formula here presented with the estimate obtained by a Chicago formula, corrected for the market differential. Any well-trained statistician who is acquainted with the methods of correlation and curve-fitting can make the necessary calculations, provided he has a reliable set of monthly average prices beginning with the fall of 1902.[16]

ESTIMATING THE PRICE OF SEED POTATOES

In estimating the price of potatoes intended for seed, the factors to be considered vary with the variety. Seed potatoes of the standard late crop varieties may be looked upon as table potatoes, perhaps of a higher quality than the average.

Triumphs, on the other hand, are affected by forces very different from those which determine the price of table stock. As raised in Minnesota, they usually sell for a large discount as table potatoes and consequently are sold for that purpose only when they can not be sold for seed. Ordinarily their price is determined by the supply and the demand for that particular variety of seed only. No special study has been made of the factors determining the price of this variety of potatoes.

Early Ohio, Irish Cobbler, and similar varieties, which, tho early, are satisfactory table potatoes for winter use, fall between the two classes of seed potatoes just discussed. Occasionally they are kept relatively high in price because of the demand for seed of each particular variety, but usually their price follows closely that of table potatoes. If they have to be sold as table potatoes late in the spring, they usually move only at a discount, owing to their poorer quality late in the season.

APPLICATION OF THE FORMULA TO AN ACTUAL CASE

The price-estimating formula was worked out from data for the years 1902-03 to 1920-21, no data being available for 1921-22 at the time the work was begun. Application of the formula to estimating the price for 1921-22 gives an opportunity for illustrating its use and also for giving the formula a further test.

The yield of potatoes in 1921, as estimated by the United States Department of Agriculture, was 90.9 bushels per acre.[17] The average of the Bureau of Labor Statistics index number of wholesale prices

[16] The writer will be glad to answer questions regarding method and to furnish some of the necessary statistical data for the benefit of any competent person who has the necessary price data and wishes to calculate a price-estimating formula.

[17] Revised estimate.

was 142.[18] Placing these figures in the formula, together with the values obtained from Table VII, page 31, or from Table IX on the final page of this bulletin, we have:

$$\text{Price per cwt.} = \frac{142 \times 57.1}{1.70 \times 90.9 - 105} = \frac{8108}{155 - 105} = \frac{8108}{50} = 162 \text{ cts.}$$

The actual average (harmonic mean) price for the year was $1.57 per hundredweight, giving a difference of 5 cents between the actual price and the estimated price.

The reason for using the harmonic mean has been explained earlier in this bulletin.[19] The harmonic mean is the *average quantity sold for a dollar* expressed in terms of price. It is calculated by dividing 1 by the average price for each month ($\frac{1}{.50} = 2$, etc.) adding the figures thus obtained for each month, dividing by the number of months, and dividing 1 by the result.

SUGGESTIONS FOR A SELLING POLICY FOR FARMERS

The foregoing discussion has explained the operation of the price-determining forces and given a formula for calculating the price which is justified in any month of the season on the basis of apparent demand-and-supply conditions. Knowledge of these facts suggests the possibility that farmers and managers of coöperative associations may make additional profits by trying to sell at the right time. Some suggestions may be made along this line. Information presented in this bulletin may be used in either of two ways: (a) As a basis for a regular selling policy; or (b) as an aid to speculating on price changes.

a. An examination of Table VII and Figures 5 and 6 shows that on the average it is to be expected that the price of potatoes in April will be from 12 to 13 per cent higher than in October. This is the increase in Minneapolis and St. Paul. The percentage increase in the farm price is greater because while the market price is rising 12 per cent from 60 cents to 67 cents, the farm price may rise, for example, from 40 cents to 47 cents, which is an increase of more than 17 per cent.

Farmers (or dealers) who can make money on the average by storing potatoes, counting on such a rise in price, will do well to adopt a policy of always carrying their potatoes over until the late winter or spring. Farmers undertaking this policy should make it a practice to keep track of the quantity of potatoes put into storage each year and of the quantity which they finally sell. By doing this they may make sure that they have not underestimated the shrinkage to be counted on. Potatoes stored in a dry place lose a great deal of weight from evaporation of moisture, a factor frequently underestimated.

[18] New index number.
[19] *Cf. supra* p. 10.

A policy which may be adopted where average cost of storing does not justify holding until spring every year is that of storing in all years in which conditions are such as to promise very little shrinkage due to rot in storage. However, if conditions are similar over most of the United States, everybody will be inclined to store potatoes, with the result that prices will be little higher in the spring than in the fall.

A third possible policy, the safest of all, is to sell a certain percentage of the crop each month. Anyone who has read this bulletin with care will understand that any estimate of the price to be expected is subject to considerable error. Slight errors in yield figures are always to be expected; estimates of acreage harvested are inaccurate; loss in storage can not be predicted with any certainty. With these and other possible causes of errors in estimating prices, it is apparent that it is never possible to be sure what will happen. By distributing sales evenly throughout the season it is possible to play safe.

b. The farmer who wishes to try to judge the market, to hold his potatoes when prices appear to be lower than fundamental conditions justify, and to seize the opportunity of selling whenever prices seem as high as conditions justify or temporarily higher, should bear in mind that he is speculating. There is always too much uncertainty regarding the fundamental conditions of demand and supply to make possible any certainty as to what will happen to the price of potatoes. However, somebody must take the chance of possible loss on changes in the price of potatoes. There is no reason why farmers should not take the chance of loss (and the possibility of gain) provided they recognize that they are speculating and understand the chances they are taking.

The farmer who is planning to study the market and tries to make money by selling when it is most favorable should bear in mind two important facts:

1. The price at any time is the result of the best estimates of a large number of people as to what the price ought to be. There is never any chance of making money by "judging the market," except when the majority of these people are wrong. It frequently happens that the majority are wrong, owing to a misinterpretation of facts or to errors in what are supposed to be facts. Any one who can outguess the majority of those dealers and farmers who are trying to judge the market can make money at it. But remember, there is no money in speculation for the man who can not outguess the majority of those in the game.

2. It requires careful study to be able to judge the market well enough to avoid losses, and more to make profits. It is bad business to spend time in that way as long as an equal amount of time spent in other ways will bring certain profits. Grading

carefully, shipping uniform lots, and raising a better quality of potatoes are usually sure means of increasing profits. **Lack of care in shipping potatoes results in thousands of dollars of loss every year through rotting and freezing in transit.**

TABLE VIII

PRICE OF POTATOES PER BUSHEL IN MINNEAPOLIS AND ST. PAUL MONTHLY, 1899-1922, BY CROP YEARS—AVERAGE TABLE STOCK

	1899-1900	1900-1901	1901-1902	1902-1903	1903-1904	1904-1905	1905-1906	1906-1907
September	$0.42	$0.26	$0.83	$0.26	$0.48	$0.32	$0.36	$0.42
October	0.39	0.26	0.62	0.31	0.48	0.31	-0.41	0.40
November	0.44	0.29	0.74	0.34	0.54	0.30	0.53	0.38
December	0.51	0.37	0.76	0.37	0.57	0.30	0.52	0.35
January	0.40	0.36	0.73	0.41	0.62	0.48	0.50	0.41
February	0.40	0.45	0.70	0.39	0.88	0.27	0.46	0.39
March	0.34	0.40	0.72	0.35	0.97	0.29	0.41	0.45
April	0.25	0.35	0.81	0.32	1.02	0.23	0.53	0.49
May	0.22	0.44	0.73	0.42	0.92	0.26	0.52	0.57
Annual Av.*	$0.37	$0.35	$0.74	$0.35	$0.72	$0.31	$0.47	$0.43
Harmonic mean	$0.35	$0.34	$0.74	$0.35	$0.66	$0.30	$0.46	$0.42

	1907-1908	1908-1909	1909-1910	1910-1911	1911-1912	1912-1913	1913-1914	1914-1915
September	$0.57	$0.61	$0.46	$0.70	$0.74	$0.41	$0.63	$0.57
October	0.51	0.59	0.40	0.59	0.58	0.37	0.61	0.43
November	0.46	0.57	0.39	0.48	0.68	0.42	0.61	0.34
December	0.46	0.61	0.38	0.44	0.70	0.40	0.59	0.37
January	0.52	0.66	0.41	0.49	0.87	0.39	0.60	0.39
February	0.58	0.77	0.45	0.48	0.97	0.40	0.50	0.42
March	0.62	0.85	0.35	0.52	1.12	0.39	0.62	0.39
April	0.61	0.97	0.22	0.63	1.19	0.36	0.53	0.42
May	0.57	0.91	0.25	0.63	1.11	0.41	0.65	0.41
Annual Av.*	$0.54	$0.72	$0.36	$0.55	$0.88	$0.39	$0.61	$0.42
Harmonic mean	$0.54	$0.70	$0.35	$0.54	$0.83	$0.39	$0.61	$0.41

	1915-1916	1916-1917	1917-1918	1918-1919	1919-1920	1920-1921	1921-1922
September	$0.33	$1.12	$1.07	$1.26	$1.54	$1.19	$1.10
October	0.47	1.22	1.38	1.10	1.46	0.99	1.02
November	0.51	1.51	1.18	0.97	1.59	1.06	0.88
December	0.64	1.48	1.07	0.96	1.83	0.78	0.83
January	0.90	1.67	1.19	1.06	2.39	0.72	1.04
February	0.86	2.16	1.21	1.01	2.43	0.55	0.95
March	0.83	2.25	1.04	0.89	3.17	0.61	0.86
April	0.79	2.56	0.64	1.15	4.21	0.49	0.79
May	0.86	2.78	0.63	1.21	4.28	0.44	0.99
Annual Av.*	$0.69	$1.78	$1.05	$1.07	$2.52	$0.75	$0.95
Harmonic mean	$0.62	$1.69	$0.98	$1.06	$2.18	$0.68	$0.94

*Weighted average obtained by weighting monthly prices by the number of weeks included in each.

FORMULAS AND TABLES FOR ESTIMATING PRICE[20]

$$\text{Price per bushel} = \frac{L \times T}{2.83Y - 174} \qquad (1)$$

$$\text{Price per hundredweight} = \frac{L \times T}{1.70Y - 105} \qquad (2)$$

L = Bureau of Labor Statistics "all commodities" index number of wholesale prices, estimated average September to May.

Y = Estimated yield per acre for the United States.

T = Values differ for each year, as shown in Table IX.

The formulas give the average (harmonic mean) price for the season. Average prices for individual months may be obtained by multiplying by factors given in Table X.

TABLE IX

VALUES OF T FOR USE IN FORMULA

Year	T
1921-22	57.1
1922-23	62.9
1923-24	69.4
1924-25	77.3

TABLE X

SEASONAL VARIATION OF PRICE

Month	Per cent of average for season
September	96.2
October	88.6
November	91.7
December	93.2
January	100.3
February	106.6
March	108.3
April	111.1
May	109.9
Average (Harmonic mean)	100.0

[20] The price obtained applies to potatoes of average table quality on the wholesale market of Minneapolis and St. Paul.

The University of Minnesota
Agricultural Experiment Station

Studies on the Parasitism of Helminthosporium Sativum

By J. J. Christensen
Division of Plant Pathology and Botany

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. The figures in Tables XII, XIV, and XV are centimeters instead of cubic centimeters, as given.

The description of Fig 2, Pl. III should read:

A. *Hordeum murinum*

Check

Inoculated

B. *Agropyron tenerum*

Check

Inoculated

CONTENTS

ILLUSTRATIONS

STUDIES ON THE PARASITISM OF
HELMINTHOSPORIUM SATIVUM

By J. J. Christensen[1]

INTRODUCTION

Within the last three or four years increasing importance has been attached to cereal diseases caused by *Helminthosporium sativum* Pammel, King, and Bakke.

In 1909 Pammel (5) published a short article on a new disease of barley characterized by irregular brownish lesions on the leaves. This was followed the next year by a publication by Pammel, King, and Bakke (6) in which they attributed the cause of the spot disease to *Helminthosporium sativum n. sp.*

Bolley (1), in 1913, called attention to the seriousness of root- and foot-rots of wheat and stated that constant cropping of wheat on the same land caused wheat sickness and wheat-sick soil. He maintained that this sickness of soil was not due to lack of essential elements or to permanent excrement or poisons detrimental to plants. He stated that it was caused by fungi, especially Helminthosporium, Alternaria, Fusarium, and Colletotrichum.

In the spring of 1919 pathologists and numerous wheat growers became greatly concerned over a serious and destructive foot- and root-rot of wheat which occurred in Illinois and Indiana. This was at first thought to be the Australian Take-All, which is caused by *Ophiobolus cariceti* (B. and Br.) Sacc. However, Stevens (10) was of the opinion that the disease might be caused by *Helminthosporium sp.*

Louise J. Stakman (9), in 1920, showed that *Helminthosporium sp.*, apparently identical with *H. sativum*, caused not only spot blotch of barley, but also root-rot and seedling blight of wheat and rye. By artificial inoculations, she proved that the same fungus also readily attacked various grasses.

Hamblin (3) was of the opinion that the "foot-rot" caused by *Helminthosporium sp.* did more damage to the wheat in Australia in 1921 than did the true Take-All.

The diseases caused by *Helminthosporium sativum* appear to be very widely distributed, as inoculations made from cultures obtained . from different sections of the United States, Canada, Argentina, and

Australia produce typical symptoms on wheat, emmer, barley, and rye. The same organism was also isolated from wheat grown in Mexico. During the summer of 1921 the pathogene was isolated from specimens from North Dakota, Nebraska, Oklahoma, Texas, New Mexico, Iowa, Wisconsin, Michigan, Illinois, West Virginia, and Minnesota.

In 1919 the disease was reported from practically every important wheat growing county in Minnesota. In some localities it caused considerable losses. Some fields of wheat in Sherburne county were so badly injured that the farmers plowed them under and planted them to corn. In 1921 the disease again was serious and widespread in the state. The writer visited fields of wheat, rye, and barley in twenty important grain-growing counties. Infection was common in every field inspected. Severe infection and considerable damage were observed in several counties, especially in St. Louis, Anoka, Kittson, Pennington, Marshall, and Wilkin; and specimens were received from several other counties. In the spring of 1922 it was estimated that the disease caused a loss of from ten to twenty per cent in many fields of barley and wheat in Dakota, McLeod, and Rice counties. Heavily infected fields also were observed in Renville, Meeker, Chippewa, Polk, and Scott counties. The damage was manifested by local necrosis of the leaves and by a stunted, spindling, or rosette appearance of the infected plants and a marked rotting of the root system.

The pathogene, *Helminthosporium sativum,* then, is responsible for leaf spot, root-rot, foot-rot, and seedling blight of wheat, barley, rye, and numerous grasses. The disease caused by it apparently is becoming more widely distributed and more destructive, not only in Minnesota and other parts of the United States but also in many of the other important grain-growing countries of the world. For these reasons, it is desirable to know more about the parasitism of the fungus. The investigations reported in this bulletin include a study of the host range and biologic specialization of the fungus, the varietal resistance of its hosts, methods of overwintering, and sources of infection.

SYMPTOMS

Helminthosporium sativum attacks every part of a susceptible host. Roots, stems, leaves, spike, spikelets, and seeds all become infected. The symptoms described here have not only been observed in the field but have been produced by artificial inoculations in the greenhouse.

The first apparent symptom of the disease in the fields is a seedling blight somewhat like damping-off. The plants may be so severely attacked by the fungus at the ground line that they are quickly killed. Some of the diseased seedlings may even fail to push out of the soil, their roots and young shoots being completely rotted by the organism.

Others may develop a fairly good root system but the stems are destroyed. Still other plants may develop one or two healthy leaves, but soon die because they fail to produce roots (see Plate II). If the seeds are severely infected they may not germinate; while, if the infection is less severe, weak and spindling plants may develop.

However, the most conspicuous symptom of the disease is the distinct dwarfing of the infected plants. In heavily infected areas these stunted plants often occur in characteristic patches which are usually circular but frequently irregular in outline, and which may vary from a few feet to several rods in diameter. Similar dwarfed plants also may be found intermixed with healthy plants.

Often the basal leaves of these stunted plants arise at the ground line or even below it and they often are darker green in color than normal ones. The internodes and the first leaves are considerably shorter than those of normal plants, the primary roots are infected, and the foot of the plant is discolored by the fungus. Large chocolate-colored lesions often occur at the base of the first leaf. Occasionally one or more large spots appear on the blades of the first and second leaves, and curling of these leaves is not uncommon. Infected plants may recover and grow to maturity, or they may gradually succumb to the pathogene.

If the seedlings are not killed, the leaves of the diseased plant may become a darker green than those of normal plants. Severely infected plants usually remain dwarfed and may stool excessively. As many as thirty to forty culms are not uncommon, especially on diseased barley plants; but, as a rule, not more than half that many develop. In many cases only one or two of the culms develop normally and produce seeds (see Plate III, Fig. 1). Sometimes, however, the same organism prevents stooling by attacking the new shoots before they emerge from the sheath, or soon after. In fact, this is one of the most common symptoms observed in the wheat fields of Minnesota.

Likewise, the secondary roots are frequently infected while quite small. This results in a poor root system, in foot-rot, and in weak, spindling plants. The roots are brittle and decayed, and on attempting to pull them up, they often break at the crown and remain in the soil. Diseased plants reach varying stages of development and maturity, depending on the degree of infection and on environmental conditions. Owing to reduced root systems the nutrition of the plant is interfered with and the water supply is cut down. The heads may be poorly filled and the seeds are sometimes shriveled.

The symptoms thus far described may all result from seed or soil infection. Subsequently secondary infections also may occur. On the

leaves, these infections usually appear as numerous dark-brown, oval or irregular blotches (see Plate I). The appearance of the lesions, however, varies with the host. For instance, on einkorn and on *Bromus villosus* Forsh, the lesions have a light center bordered by a halo; and on certain varieties of rye a water-soaked leaf spot, with or without a brownish border, is produced. On *Andropogon sorghum* Brot. red, oval lesions develop, while on *Agropyron repens* (L.) Beauv. the lesions are usually elongated and black. Sometimes two or even more types of infection appear on the same leaf. The size of the lesions varies greatly on the same leaf, ranging from very small to 3 by 20 millimeters or more in size. The coalescence of these spots often results in the death of part or all of the infected leaf.

The fungus also causes similar lesions on the stem, glumes, awns, and even on the seeds. The pathogene fruits very abundantly on the nodes, giving them a black velvety appearance. The internodes seldom become very much darkened, except near the base of the culms, altho occasionally all of them may be much discolored.

The seeds also may be discolored, or the entire head or portions of it may be blighted. The ovary of the floret may be attacked at any stage in its development, and the kernel either may fail to form, or, when formed, it may be badly shrunken. Generally the germ end of the seed is most conspicuously discolored. Under favorable conditions, the fungus fruits luxuriantly on undeveloped kernels. Sometimes the rachis is infected and this prevents proper filling of the parts above the lesion. The causal organism fruits very abundantly in nature on the glumes of the spikelets of wheat, emmer, spelt, and einkorn.

All the enumerated symptoms can be caused by the same fungus, *Helminthosporium sativum* Pammel, King, and Bakke. This organism was found to be constantly associated with the various lesions on the different parts of the plants. Hundreds of isolations were made from the infected plants collected, not only in Minnesota and adjoining states, but also in various parts of the United States and other countries. The fungus was isolated from many naturally infected cereals and grasses, including several varieties of rye and corn, 20 varieties of barley, and 70 varieties of wheat. In addition, the same, or at least a very similar organism, was isolated from the following grasses:

Alopecurus pratensis L., *Agropyron caninum* (L.) Beauv., *A. disertorum* Schult., *A. repens* (L.) Beauv., *A. smithii* Rydb., *A. tenerum* Vasey, *Andropogon furcatus* Muhl., *A. sorghum sudanensis* Piper, *Bromus inermis* Leyss., *Calamagrostis canadensis* (Michx.) Beauv., *Dactylis glomerata* L., *Digitaria sanguinalis* Scop., *Echinochloa crusgalli* (L.) Beauv., *Elymus canadensis* L., *E. glaucus* Buckl., *E. robustus*

Scribn. and J. G. Sm., *E. straitus* Willd., *E. virginicus* L., *Hordeum jubatum* L., *H. pusillum* Nutt., *Hystrix patula* Moench., *Lolium sp.* L., *Muhlenbergia sp.,* Schreb., *Panicum capillare* L., *Phalaris arundinacea* L., *Phragmites phragmites* L. Karst., *Setaria glauca* L., *S. italica* Beauv., *S. viridis* L., *Sorghum halapense* (L.) Pers., *Stipa spartea* Trin., and *Zizania palustris* L. The same fungus was re-isolated from several hundred plants which became diseased as a result of artificial inoculation in the field and greenhouse.

Cross-inoculations with several strains of Helminthosporium obtained from wheat, barley, and rye all produced the typical "spot-blotch" on barley and the same organism also infected wheat, rye, and many grasses.

Plants were grown in more than 600 pots of soil which had been inoculated with *Helminthosporium sativum* and in addition, thousands of plants representing many genera, species, and varieties were sprayed with spore suspensions. By this means the symptoms which have been described were obtained repeatedly.

Thus, the disease was produced in both the field and the greenhouse by inoculating seed and soil, and by spraying the plants with a suspension of spores. In the laboratory, infected seeds developed diseased seedlings when germinated on agar (see Plate IV, Fig. 1) or on sterile blotting paper, and in the greenhouse by planting them in sterile sand or loam. The disease also was reproduced in the greenhouse by using soil from fields where severe infection had occurred.

CULTURAL CHARACTERS AND BIOLOGICAL SPECIALIZATION

No general description of the morphological or cultural characteristics can be given because transfers from the same culture produce different types of growth and wide variation in size of spores on different media and under different environmental conditions. Moreover, there are several physiological races or biologic forms of *Helminthosporium sativum,* each of which produces a different type of growth on a given medium.

While studying cultural characteristics of two strains of *Helminthosporium sativum* derived from single spores isolated from spot blotch on barley, it was observed that marked variations occurred when they were grown on the same medium under the same conditions. For this reason the characteristics of two cultures from barley, one from rye, and one from wheat, all derived from single spores, were compared on green bean agar, on one per cent potato dextrose agar, and on carrot agar. These comparative studies were made in petri dishes

of the same diameter. Tubes from which the plates were poured contained ten cubic centimeters of medium, and two tubes were poured into each petri dish. Sixteen plates of each kind of medium were used, four of each being inoculated with each culture of *Helminthosporium sativum*. Inoculations were made from cultures of the same age, and only one tube of each culture was used in inoculating the twelve plates of the three different media. The inoculum consisted of a small portion of the potato agar containing mycelium and spores, and as nearly as possible the same amount was used in each case. The plates were placed in a dark incubator, in which the temperature varied between 20° and 22°C. The fungus was permitted to grow for three or four days before any notes were taken, in order to eliminate any effect due to differences in the amount of inoculum in the different cultures.

It is evident from Plates V and VI and from Table I that the cultural characters of the four biologic forms greatly differ from each other on the same medium. The cultural characters of the same form are also different on different media, for instance, Form IV produces a white growth on green bean agar, but a black colony on potato dextrose agar. It was repeatedly observed that the color and nature of growth on a given medium varied with the temperature, amount of moisture, and other factors. But the colonies of the same form on the four plates were consistent. Thus the type of growth under the same conditions depends first on the form and second on the medium used. Plates V and VI and Table I indicate that two strains may appear similar when grown on one type of medium, but may differ markedly when transferred to a different medium. For instance, Forms I and IV are very similar on potato dextrose but are strikingly different on green bean agar.

As is brought out in Table I, there also is considerable variation in the rates of growth of the four cultures on the same and on different media. On potato dextrose Form I increased 3.44 centimeters in twenty-four hours, while Form II increased only 0.94 cm. in the same time. On green bean agar, however, the latter strain grew more than 5 cm. during the same period. Thus, the rate of growth at a uniform temperature depends on the kind of medium as well as on the form used.

Comparative inoculations were made with these four biologic forms on wheat, barley, rye, and grasses. All caused typical spot blotch on barley, but differed in the severity of infection which they produced on all the hosts. The exact differences in the pathogenicity of the four forms, however, can not be given definitely.

TABLE I

COMPARATIVE CULTURAL CHARACTERISTICS OF FOUR BIOLOGIC FORMS OF *H. sativum*, WHEN GROWN ON THE SAME AND DIFFERENT MEDIA UNDER THE SAME CONDITIONS

Biologic forms	Rate of growth per day*			Color of colonies			Character of growth†		
	Potato dextrose agar	Green bean agar	Carrot agar	Potato dextrose agar	Green bean agar	Carrot agar	Potato dextrose agar	Green bean agar	Carrot agar
	cm.	cm.	cm.						
I Isolated from rye	3.44	7.62	2.27	Grayish black	Olive gray	Dark blue-green	Regular; very finely stippled; zonation sharp	Regular; few large zones	Very irregular
II Isolated from barley	4.31	6.40	2.64	Grayish black	Grayish black	Dark blue-green	Regular; coarsely stippled; zonation sharp	Regular; tufts common; zonation not as sharp as in Form I	Slightly irregular; considerable guttation
III Isolated from barley	0.94	5.12	2.25	Gray	White, black and gray intermixed	Grayish to dull yellow	Very irregular; no zonation	Irregular; cones of varied color; zonation not sharp	Irregular; considerable aerial mycelium
IV Isolated from wheat (Culture obtained from Dr. F. L. Stevens)	3.56	7.06	1.44	Grayish black	White	Dark blue-green	Slightly irregular; zonation very sharp; very little aerial mycelium	Regular; white aerial mycelium; no sporulation	Dense; very little aerial mycelium

* Average increase in diameter per day over a period of four days.

† Six to ten days after inoculations.

The facts that these cultures differ physiologically, as is indicated by their different reactions to the same medium under uniform conditions, and that they react differently on various hosts, proves that biologic specialization exists in *Helminthosporium sativum* and that the four cultures obtained from single spore isolations and used in this investigation must be regarded as four distinct biologic forms of this species.

The variation of one form under different conditions, or of different forms under the same conditions, is very marked. A technical description of the organism, therefore, is of little value, unless the exact conditions under which it was grown are definitely known.

MORPHOLOGY OF THE SPORES

In the laboratory, Form I was found to sporulate very abundantly on boiled rice, wheat, barley, and green beans, and on one per cent potato dextrose agar. In nature, the fungus apparently fruits most luxuriantly on nodes of susceptible cereals. The conidia are usually solitary but they also have been observed in chains on potato dextrose agar. In cultures on potato dextrose agar, conidia were often seen germinating and giving rise to smaller ones; these in turn produced still smaller ones, and so on.

The conidia have a thin epispore dark-olive or brown in color, and a hyaline endospore. The shape is variable as is shown in Plate IV, Figures 2 and 3. The spores are typically spindle-shaped, with rounded ends, but frequently the widest point is nearer one end than the other. The shape ranges from fusoid to clavate or cylindric. Slight variations in shape occur among the spores of different forms and even among those of the same form with varying conditions of environment and substratum. The spores are often curved, and occasionally are irregular.

The number of septa in the spores varies with the biologic form and with the medium on which the fungus is grown. Two hundred spores of each form were observed. Table II summarizes the number of septa in the spores of the four biologic forms which were grown on heads of Marquis wheat under the same conditions. Table III gives similar data for Form I on different media. Each class in Tables II and III differs by one septum.

Table II indicates that the four forms differ in septation. The mode of Form IV is at eight septa, while that of Form III is at six. There is but little difference in the number of septa in spores of different biologic forms which have been grown under the same conditions. There is greater variation within a single form when grown under different environmental conditions. This is brought out by Table III.

TABLE II

VARIABILITY IN NUMBER OF SEPTA OF CONIDIA OF FOUR DIFFERENT BIOLOGIC FORMS OF *H. sativum* PRODUCED ON HEADS OF WHEAT UNDER THE SAME CONDITIONS

Biologic forms	Septation classes													Range	Mode
	0	1	2	3	4	5	6	7	8	9	10	11	12		
I	3	0	0	3	15	19	37	52	39	20	10	2	..	0-11	7
II	..	..	1	2	8	9	31	56	51	29	9	3	1	2-12	7
III	4	5	6	17	30	40	53	28	10	4	3	..	..	0-10	6
IV	..	..	..	1	3	9	25	58	64	29	8	3	..	3-11	8

TABLE III

VARIABILITY IN NUMBER OF SEPTA OF CONDIA OF BIOLOGIC FORM I OF *H. sativum* PRODUCED ON DIFFERENT MEDIA

Culture medium	Septation classes												Range	Mode
	0	1	2	3	4	5	6	7	8	9	10	11		
Head of wheat...........	3	0	0	3	15	19	37	52	39	20	10	2	0-11	7
Potato dextrose* (A)......	3	8	10	15	29	48	46	25	11	4	1	..	0-10	5
Potato dextrose (B).......	26	47	48	24	24	13	12	5	1	..	..	..	0-8	2

* Potato dextrose (A) and (B) were made up according to the same formula but at different times.

Table IV summarizes the lengths of five hundred spores for each of the four biologic forms of *Helminthosporium sativum* from cultures grown under the same conditions on heads of wheat. Table V gives the lengths of five hundred spores of Form I on different media. In Tables IV and V the spore lengths are grouped into classes, the range of each class being ten microns, and from these were computed the biometrical constants with their probable errors for the different biologic forms on the same medium and for Form I on different media.
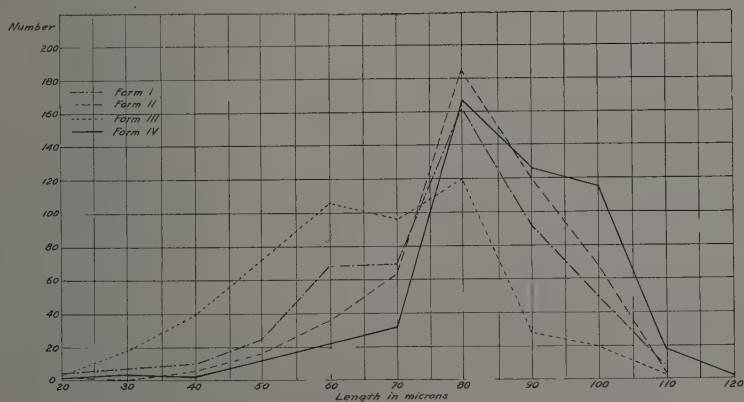
Fig. 1. Difference in Length of Spores of Four Biologic Forms of *H. sativum* Developed on Heads of Wheat Under the Same Condition

TABLE IV

VARIATIONS AND CONSTANTS FOR LENGTH OF SPORES OF BIOLOGIC FORMS OF *H. sativum* DEVELOPED ON HEADS OF WHEAT UNDER THE SAME CONDITIONS

| Biologic forms | Spore-length classes (in microns) | | | | | | | | | | | Range | Constants | | | |
	20	30	40	50	60	70	80	90	100	110	120		Mode	Means	Standard deviation	Coefficient variability
I	5	8	10	25	68	69	163	93	50	9	...	11.40— 114.00	80	76.60 ± 0.51	16.86 ± 0.36	22.01 ± 0.47
II	1	0	6	17	36	65	184	119	69	3	...	38.00— 106.40	80	80.96 ± 0.52	13.50 ± 0.41	16.67 ± 0.36
III	3	19	41	74	105	96	120	30	10	2	...	15.20— 106.40	80	65.02 ± 0.50	16.65 ± 0.35	25.60 ± 0.55
IV	1	3	2	12	22	32	166	126	116	18	2	26.60— 117.80	80	85.58 ± 0.43	14.16 ± 0.30	16.53 ± 0.35

TABLE V

VARIATIONS AND CONSTANTS FOR LENGTH OF SPORES OF BIOLOGIC FORM I OF *H. sativum* PRODUCED ON DIFFERENT MEDIA

| Culture medium | Spore-length classes (in microns) | | | | | | | | | | | Length limits | Constants | | | |
	10	20	30	40	50	60	70	80	90	100	110		Mode	Means	Standard deviation	Coefficient variability
Head of wheat	...	5	8	10	25	68	69	163	93	50	9	15.20— 114.00	80	76.60 ± 0.51	16.86 ± 0.36	22.01 ± 0.47
Potato dextrose* (A)	...	24	41	21	96	161	85	62	8	1	1	15.20— 114.00	60	57.70 ± 0.50	16.45 ± 0.35	28.50 ± 0.61
Potato dextrose* (B)	3	169	197	40	42	18	13	14	3	1	...	11.40— 106.40	30	33.00 ± 0.47	15.62 ± 0.33	47.33 ± 1.09

* Potato dextrose (A) and (B) were made up according to the same formula, but at different times.

The spore lengths represented in Tables IV and V are plotted in Figures 1 and 2. All four forms have the same mode, namely, 80 microns. The modes in Table V and the curves in Figure 2 show at a glance that the length of spore of a single form varies greatly on different media. For example the modal length of Form I grown on a head of wheat is 80 microns, on potato dextrose in one case, 60 microns; in the other, 30 microns.
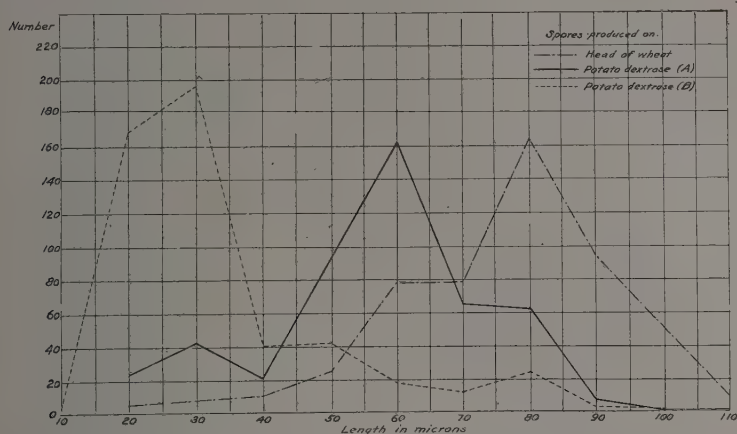
Fig. 2. Difference in Length of Spores of Form I of *H. sativum* Developed on Different Media

TABLE VI

SUMMARY OF DIFFERENCES IN THE MEAN LENGTH OF SPORES OF BIOLOGIC FORMS OF *H. sativum*

Biologic forms	Difference in mean length (in microns)	Difference in mean length divided by probable error of the difference
I and II	4.36±0.65	6.71
I and III	11.58±0.71	16.31
I and IV	8.98±0.67	13.40
II and III	15.94±0.65	24.52
II and IV	4.62±0.59	7.83
III and IV	20.56±0.66	31.51

TABLE VII

SUMMARY OF DIFFERENCES IN THE MEAN LENGTH OF THE SPORES OF BIOLOGIC FORM I OF *H. sativum* PRODUCED ON DIFFERENT MEDIA

Culture medium	Difference in mean length (in microns)	Difference in mean length divided by probable error of the difference
Head of wheat and potato dextrose* (A).......	18.90±0.71	26.61
Head of wheat and potato dextrose (B)........	43.60±0.69	63.18
Potato dextrose (A) and Potato dextrose (B)..	24.70±0.68	36.32

* Potato dextrose (A) and (B) were made up according to the same formula but at different times.

Table VI gives the differences in the mean lengths of conidia of the four biologic forms of *Helminthosporium sativum* and the ratios between these differences and their probable errors. Table VII summarizes similar data for Form I grown under different conditions. The differences between the mean lengths of the spores of the four biologic forms are significant in every case. The differences in mean spore length of the same Form I on different media, given in Table VII, are surely very significant. In one case the mean is more than sixty-three times as great as the probable error.

TABLE VIII

VARIABILITY IN WIDTH OF SPORES OF THE DIFFERENT BIOLOGIC FORMS OF *H. sativum* PRODUCED ON HEADS OF WHEAT UNDER THE SAME CONDITIONS

Biologic forms	Spore-width classes (in microns)						Range	Mode
	11.40	15.20	19.00	22.80	26.60	30.40		
I	.....	4	60	190	44	2	15.20–30.40	22.80
II	.....	1	27	194	77	1	15.20–30.40	22.80
III	2	39	150	94	15	.....	11.40–26.60	19.00
IV	1	3	48	221	27	.....	11.40–26.60	22.80

TABLE IX

VARIABILITY IN WIDTH OF SPORES OF BIOLOGIC FORM I OF *H. sativum* ON DIFFERENT MEDIA

Culture medium	Spore-width classes (in microns)						Range	Mode
	11.40	15.20	19.00	22.80	26.60	30.40		
Head of wheat...........	.....	4	60	190	44	2	15.20–30.40	22.80
Potato dextrose* (A).....	8	25	122	131	14	.....	11.40–26.60	22.80
Potato dextrose (B)......	78	121	63	34	4	.....	11.40–26.60	15.20

* Potato dextrose (A) and (B) were made up according to the same formula, but at different times.

Table VIII summarizes the variation in width of spores of the different biologic forms. Three hundred spores were measured in every case, the spores being the same that were used for measurements of length. Table IX gives similar results for Form I when grown on heads of wheat and potato dextrose. The range of each class in Tables VIII and IX is 3.8 microns. It will be noticed that Form III, which had practically the same modal length as Form I, had a modal width 3.8 microns smaller than that of the other three forms. In Form I marked variation in width is evident between spores grown on a head of wheat and those grown on potato dextrose.

The size, shape, and degree of curvature of spores of the same form vary considerably on different media and under different conditions. This variation is so marked that one would be inclined to

consider the extreme cases not merely as different biologic forms of one species but rather as distinct morphological species. For example, the mode of Form I is 33 microns on potato dextrose (B), while on wheat heads it is 80 microns. A large number of spores must, therefore, be measured in order to obtain reliable results, and any given spore dimension can be applied only to spores produced on a specific medium, under known conditions. On potato dextrose (A) the measurements of Form I agree fairly well with those given by Louise J. Stakman (9). On the head of wheat they approach the measurements obtained by Pammel, King, and Bakke (6), but resemble more closely those mentioned by Stevens (10).

PATHOGENICITY STUDIES
METHODS AND MATERIALS

The organism used in the following experiments was isolated from rye seed unless otherwise indicated. Each strain of the fungus used was derived from a single spore isolation.

The fungus used for leaf inoculations was grown on potato dextrose agar. The spores were carefully scraped off into water and the suspension was poured through cheesecloth to remove any bits of medium that were accidentally loosened during the process. The spores were then applied with a small Daisy hand sprayer. The plants inoculated in the greenhouse were well moistened and special pains were taken to keep a constant film of water on them during incubation.

After inoculation, the plants were placed in a thoroly cleaned incubation chamber for about seventy hours. These chambers consisted of large galvanized iron cylinders with glass tops and fitted closely into a pan which contained an inch or two of water. During warm, sunny weather the tops of the incubation chambers were covered with paper to keep the temperature from rising too high.

All seeds used in the following soil experiments were first moistened with 50 per cent alcohol and then immersed from two to four minutes in a 1:1000 solution of mercuric bichloride, after which they were rinsed in water. The soil and pots used were autoclaved from two to five hours. In some cases a spore suspension was added to the sterile soil, but in most cases the fungus was grown on autoclaved media and this was mixed with the steamed soil. Only the autoclaved medium was added to the check pots. The plants were kept fairly moist and their positions were interchanged from time to time in order to eliminate, as far as possible, environmental differences.

The following method was used in isolating the fungus: Seeds or pieces of the plant tissue from one to two centimeters long, were disinfected first by immersing them for half a minute in 50 per cent

ethyl or methyl alcohol and then in mercuric bichloride 1:1000 for
from three to four minutes, after which they were rinsed in alcohol.
The pieces were then plated out on potato dextrose agar in petri dishes.
Isolations as a rule were made in duplicate.

Four-inch pots were used except when it was desired to grow
plants to maturity, when eight-inch pots were used. The pots in which
cereals were grown contained about twenty plants, but many more
grass plants were grown in each pot.

The seeds of the grasses used were obtained from the grass gardens
of the Bureau of Plant Industry at Lafayette, Ind., and Berkeley,
Calif. Some were obtained from the Minnesota Seed Laboratory,
and a few were collected locally. The seeds of corn and cereals were
obtained from the Agronomy division, University of Minnesota, except
the club wheat, which was obtained from the Washington State Agri-
cultural Experiment Station.

INOCULATION EXPERIMENTS
HOST RANGE

The results of spraying cereals and grasses in the greenhouse and
in the field with a spore suspension of *Helminthosporium sativum* are
summarized in Table X. In all, 22 species and several varieties of
wheat, oats, barley, rye, and corn, and 112 species of grasses were
inoculated. All these species comprised 54 genera. Of the 134 species,
98 were successfully infected in the greenhouse. Fifty-eight were very
susceptible, 40 were somewhat resistant, and the remaining 36 appeared
to be immune.

Of the 66 species inoculated in the field, 57 became infected. All
the species infected in the field were also infected in the greenhouse.
Seven of the 9 species which were immune in the field did not become
infected in the greenhouse, while the other 2 were slightly infected.

The degree of susceptibility or resistance was not based on the
size or character of the lesions produced, but on the number of lesions
and the effect of the fungus on the plant as a whole. When the plant
was so severely attacked by the organism that numerous lesions were
developed and the growth of the plant was either checked or inhibited,
it was considered to be susceptible. Susceptible plants are indicated
by the symbol H (heavy), while those less severely attacked are
designated by M (medium). In cases where the presence of the
fungus interfered only slightly with growth and development of the
plant and only a few lesions were produced, the plant was considered
to be resistant. Resistant plants are designated by L (light), Tr.
(trace), and O (absence of infection). At times relatively small dead
areas appeared as the only apparent indication of infection and the

symbol Fl. (flecks) was used to indicate this condition. Plus and minus signs are used to indicate slight variation within each class.

From Table X it will be noticed that the most susceptible cereals are wheat, barley, and rye, and that different species of oats and corn are practically all immune. The following common grasses are very susceptible: *Setaria viridis, Hystrix patula, Chloris verticillata* and various species of *Agropyron, Bromus, Elymus, Festuca, Hordeum,* and *Lolium.* The following are immune or extremely resistant: *Phleum pratense, Arrhenatherum elatius, Alopecurus pratensis, Koeleria cristata,* and species of *Phalaris, Poa,* and *Agrostis.*

The results shown in Table X establish the fact that there is a marked difference in the susceptibility of plants at different ages. For instance, *Bromus ciliatus* and *B. Kalmii,* inoculated when ninety-three days old, developed only a trace of infection, and eighteen days later similar plants were very susceptible. Numerous similar examples could be given, but in each case the resistance seems to be correlated with the stage of development of the tissue rather than with its actual age. Louise J. Stakman (9) called attention to similar results from inoculation experiments on wheat. Numerous field and greenhouse observations proved that plants are most susceptible to secondary infection after heading. In fact, spots on the stems and the characteristic blackening of the nodes seldom occur until after the plants are headed. Thus a plant may be immune or fairly resistant while small, but later prove extremely susceptible.

Typical lesions are developed on blades, sheaths, culms, glumes, seeds, and awns of cereals and grasses. Numerous inoculations and re-isolations of the fungus confirmed this conclusion. The organism was also repeatedly isolated from all the parts of naturally infected hosts mentioned above. This agrees with the statement made by Louise J. Stakman (9) that all parts of the host are susceptible.

CROSS INOCULATIONS

Several series of cross-inoculations with single spore strains of *Helminthosporium sativum* from wheat and barley produced the typical spot blotch on barley and, in general, gave results similar to those obtained with the strain isolated from rye. Helminthosporium strains obtained from Argentina, Canada, and Australia, not derived, however, from single spores, likewise caused typical spot blotch on barley and attacked the common wheats, durums, emmer, and rye in the same manner as did the barley strains.

TABLE X

RESULTS OF INOCULATING CEREALS AND GRASSES WITH *H. sativum* P., K., and B.

Plants inoculated	Greenhouse inoculations*				Field inoculations
	Series 1		Series 2		
	Age, days	Degree of infection†	Age, days	Degree of infection†	Degree of infection†
Wheat					
Triticum compactum					
Little Club C. I. 4066	46	H	62	H	H
Triticum dicoccum					
Emmer C. I. 3686	46	H	104	H	H+
Khapli C. I. 4013	44	L	121	H	H
Triticum durum					
Arnautka C. I. 4072	47	L	103	L	M+
Monad C. I. 3320	91	M	121	M	H
Triticum monococcum					
Einkorn C. I. 2433	46	H	85	H	H
Triticum polonicum					
Polish, Selection	63	H	102	H	‡
Triticum spelta					
Beardless spelt, Selection	72	M	88	M+	M—
Triticum vulgare					
Kanred C. I. 5146	44	L	106	H	M—
Marquis C. I. 3641	44	H	106	H	L
Oats					
Avena brevis					
Selection	66	O	73	O	
Avena fatua					
Wild oats	66	O	73	O	
Avena nuda					
Selection	66	O	73	O	
Avena sativa					
Ligowa, Minn. No. 281	66	O	73	O	
Victory, Minn. No. 514	99	Tr	130	Fl	
Avena sativa orientalis					
Green Mountain, Selection	66	O	73	O	
Avena sterilis					
Red Rust Proof, Selection	66	O	73	O	
Avena strigosa, Selection	66	O	73	O	
Barley					
Hordeum distichon palmella					
Chevalier C. I. 278	32	M—	50	H—	H—
Svanhals, Selection	32	L+	50	H—	H+
Hordeum vulgare pallidum					
Manchuria, Minn. No. 184	64	L	84	H—	L+
Bay Brewing, Selection	44	M—	66	H	H+
Hordeum vulgare trifurcatum					
Nepal C. I. 262	64	L	68	H—	H
Rye					
Secale cereale					
Swedish Rye, Minn. No. 2	31	L	110	M+	L—
Wisconsin Pedigree, Minn. No. 84	85	Tr+	101	L—	M—

* The plants were sprayed with a suspension of spores.

† H=heavy infection; M=moderate infection; L=light infection; Tr=trace infection; O=no infection; Fl=flecks.

‡ A blank indicates that no plants were inoculated.

TABLE X—*Continued*

RESULTS OF INOCULATING CEREALS AND GRASSES WITH *H. sativum* P., K., and B.

| Plants inoculated | Greenhouse inoculations* | | | | Field inoculations |
| | Series 1 | | Series 2 | | |
	Age, days	Degree of infection†	Age, days	Degree of infection†	Degree of infection†
Corn					
Zea mays everta					
White rice popcorn	29	O	38	Tr	
Zea mays indurata					
King Philip	29	O	38	Fl	
Longfellow	29	O	38	O	
Zea mays indentata					
Minn. No. 13	29	O	38	O	
Rustler	29	O	38	O	
Zea mays saccharata					
Crosby	29	Fl	38	Tr	
Country Gentleman	29	Fl	38	Fl	
Grasses					
Agropyron caninum (L.) Beauv.	104	H	105	H+	
Agropyron cristatum J. Gaert.	104	L	152	M+	
Agropyron disertorum Schult.	74	L	102	H+	
Agropyron repens (L.) Beauv.	104	M	128	M	
Agropyron smithii Rydb.	104	L	128	L	
Agropyron spicatum (Pursh.) Scribn. and Smith	102	H —	156	H	
Agropyron tenerum Vasey.	40	M	55	H+	
Agropyron tenerum longifolium Scribn. and Smith	40	H	105	H	
Agrostis alba L.	104	O	128	O	O
Agrostis palustris Huds.	102	O	156	O	
Agrostis stolonifera L.	87	O	115	O	
Aira caryophyllea (L.) Nash.	102	O	156	O	
Alopecurus pratensis L.	104	Tr	128	Tr	L+
Andropogon sorghum Brot.	30	L—	128	M	
Andropogon sorghum sudanensis Piper	50	L	134	L+	
Anthoxanthum odoratum L.	102	L	128	L	M
Arrhenatherum elatius (L.) Beauv.	104	O	126	O	O
Arundinaria sp. Michx.	30	L—	50	Tr	
Avena barbata Brot.	104	O	108	O	
Bechmania erucaeformis (L.) Beauv.	136	Tr			Tr
Briza media L.	104	Tr	118	Tr	H
Bromus altissimus Pursh.	93	Tr	111	M	H
Bromus arvensis L.	93	Tr	111	M	H
Bromus brizaeformis Fisch. and Mey.	70	Tr	105	L+	M
Bromus ciliatus L.	93	Tr	111	H	H
Bromus hordeaceus L.	33	L			
Bromus inermis Leyss.	144	L	156	M	M
Bromus japonicus Thunb.	93	O	111	Tr	L
Bromus kalmii Gray	93	Tr	111	H	H
Bromus langinosus Poir.	33	L—	102	L+	M
Bromus marginatus Nees.	33	Tr	102	L+	H
Bromus mollis L.	93	Tr	111	L	M
Bromus porteri (Coult.) Nash.	93	O	111	M	H
Bromus pumpellianus Scribn.	100	Tr	150	L	H

* The plants were sprayed with a suspension of spores.

† H=heavy infection; M=moderate infection; L=light infection; Tr=trace infection; O=no infection; Fl=flecks.

TABLE X—*Continued*

RESULTS OF INOCULATING CEREALS AND GRASSES WITH *H. sativum* P., K., and B.

| Plants inoculated | Greenhouse inoculations* | | | | Field inoculations |
| | Series 1 | | Series 2 | | |
	Age, days	Degree of infection†	Age, days	Degree of infection†	Degree of infection†
Grasses—Continued					
Bromus purgans L.	93	Tr	111	H	H
Bromus rubens L.	33	L	102	L+	L
Bromus secalinus L.	93	L	111	L	M
Bromus sterilis L.	33	M	100	L	H
Bromus tectorum L.	104	M	128	M	M
Bromus unioloides(Willd.)H.B.K.	69	L	73	L	H
Bromus villosus Forsh.	69	L	102	L	
Capriola dactylon (L.) Kuntze	136	L	136	M—	
Cenchsus echinatus L.	55	L—.	70	M+	Tr
Chloris gayana Kunth.	70	L—	102	L—	L—
Chloris verticillata Nutt.	118	H	130	H	
Chloris virgata Swartz.	70	M+			L+
Cinna arundinacea L.	75	O	150	O	
Cynosurus cristatus L.	136	O	150	O	
Dactylis glomerata L.	125	O	143	Tr	
Danthonia intermedia Vasey.	90	Tr	102	L	L—
Deschampsia elongata (Hook.) Munro	102	M	152	L+	
Deschampsia flexuosa V. L. Trin.	136	O	152	O	
Deyeuxia Forsteri Kunth.	77	O	87	O	
Digitaria humifusa Pers.	70	O	102	O	
Echinochloa crusgalli (L.) Beauv.	33	Tr	116	L	L
Echinochloa crusgalli zelayensis Hitchc.	33	L—	102	L	M+
Elymus canadensis L.	63	M—			
Elymus robustus Scribn. and J. J. Sm.	86	M+	136	H—	
Elymus virginicus L.	144	M	166	H	H
Eragrostis abyssinia Schrad.	75	O	136	O	O
Euchlaena mexicana Schrad.	30	Tr+	42	L+	
Festuca confinis Vasey	90	L	122	H	L—
Festuca dumetorum Phil.	104	L	122	Tr	M
Festuca elatior L.	75	Tr+	122	M	M+
Festuca myuros L.	33	O	105	O	
Festuca octoflora Walt.	122	L	156	M—	
Festuca ovina L.	104	L			
Festuca rubra L.	125	Tr	125	Tr	O
Gastridium lendigerum (Gouan) Schinz and Thell.	55	O	102	O	
Glyceria nervata (Willd.) Trin.	144	O	162	Tr—	
Holcus lanatus L.	104	M	162	L	H
Hordeum jubatum L.	104	L	117	L—	M
Hordeum murinum L.	144	M	117	M	H
Hordeum pusillum Nutt.	104	L	117	M	
Hystrix patula Moench.	104	H	117	H	H
Koeleria cristata (L.) Pers.	144	O			H
Lolium italicum R. Br.	87	M	90	L	O
Lolium perenne L.	104	M	122	L	H
Lolium subulatum Vis.	33	L	105	L+	H
Lolium temulentum L.	102	M—	163	M	H

† H=heavy infection; M=moderate infection; L=light infection; Tr=trace infection; O=no infection; Fl=flecks.

TABLE X—*Continued*

RESULTS OF INOCULATING CEREALS AND GRASSES WITH *H. sativum* P., K., and B.

| Plants inoculated | Greenhouse inoculations* | | | | Field inoculations |
| | Series 1 | | Series 2 | | |
	Age, days	Degree of infection†	Age, days	Degree of infection†	Degree of infection†
Grasses—Continued					
Muhlenbergia racemosa (Michx.) M.S.P.	104	L	104	M	
Oryzopsis miliacea Davy.	102	H	156	H+	
Panicum plicatum Lam.	75	L+	156	H+	
Panicum frumentaceum Roxb.	55	Tr	70	L—	
Pappohorum vaginatum Buckl.	100	O	120	M	
Papsalum setaceum Michx.	136	O	152	O	
Pennisetum villosum R. Br.	40	Tr	55	L—	O
Phalaris arundinacea L.	30	O			L—
Phalaris bulbosa Tenore.	87	O	102	Tr+	L—
Phalaris caroliniana Walt.	102	O	156	O	
Phalaris minor Retz.	104	O	164	O	
Phleum pratense L.	105	O	111	O	O
Poa·annua L.	55	O	156	O	
Poa brachyphylla Schultes	104	O	122	O	
Poa nemoralis L.	104	O	122	O	
Poa palustris L.	156	O	156	O	
Poa pratensis L.	104	O	122	O	
Poa triflora Gilib.	104	O	122	O	O
Poa trivalis L.	104	O	122	O	
Polypogon littoralis J. E. Smith	70	O	105	O	
Polypogon maritimus Willd.	156	O	156	O	
Polypogon monspeliensis (L.) Desf.	70	L	100	Tr	
Puccinella airoides (Nutt.) Wats. and Coult.	104	M	122	L	
Puccinella simplex Scribn.	136	M—	136	M	
Saccharum officinarum L.	30	M	104	H—	M
Setaria glauca (L.) Beauv.	33	L	70	L	M
Setaria viridis (L.) Beauv.	70	H—	104	H	M
Sphenopholis obtusata (Michx.) Scribn.	104	O	122	O	O
Sporobolus cryptandrus (Tor.) Gray	136	Tr	150	Tr	
Stipa sp. L.	33	L	87	Tr	
Triodia albescens Vasey	70	O	87	Tr	
Triticum aegilops Beauv.	33	H+	105	H+	H+

† H=heavy infection; M=moderate infection; L=light infection; Tr=trace infection; O=no infection; Fl=flecks.

SOIL INFECTION EXPERIMENTS
ARTIFICIALLY INOCULATED SOIL

Seven varieties of wheat were inoculated, namely, Marquis, C. I. 3641; Kota, C. I. 5878; Kanred, C. I. 5146; Mindum, C. I. 5296; Acme, C. I. 5284; Monad, C. I. 3320; and Red Durum, Selection. The fungus was grown on autoclaved oatmeal, and both the fungus and the medium were mixed with the sterile soil. Uninoculated oatmeal was added to the checks.

The inoculated plants came up more slowly than those which had not been inoculated and the first leaf often developed typical leaf spots. Within a few days the browning of the basal sheath began to appear. The roots became brown and several of the plants died. The mortality among Marquis, Red Durum, and Kota plants was especially high. (See Plate VII, Fig. 2.) Mindum and Kanred appeared to be most resistant, while Acme was moderately susceptible. As some of the seeds used were already infected with Helminthosporium, a few of the check plants also became diseased.

In a similar but more extensive experiment, Marquis and Kanred wheats were used. Fifteen pots of each were inoculated as above, except that the fungus was grown on sterilized wheat instead of on oatmeal. In preparing this medium, dry wheat was barely covered with water and autoclaved for forty-five minutes. When the secondary roots were fairly well formed, the soil was carefully removed and the roots were washed clean in water. The root system of Kanred was usually about twice as extensive as that of Marquis. The roots of Kanred also were but slightly infected, while those of Marquis were usually quite heavily infected and broke off easily at the base of the stem.

On February 13, 1921, another series of seeds were inoculated like those in the previous experiment. In this case the fungus was grown on potato dextrose agar and this was added to the soil. The results are given in Table XI. The number of brown basal sheaths is rather low, as the notes were taken a few days too early to give the best results. Probably all the basal sheaths of the inoculated plants were brown at this time, but had as yet not made their appearance above the ground line, for a week later all the plants in the inoculated soil were characteristically discolored. There were lesions on the sheaths and roots of all the plants that were examined. The basal sheaths of the check plants of rye and wheat became somewhat discolored. This discoloration was undoubtedly due to physiological rather than to parasitic causes.

From Table XI it can readily be seen that the number of primary lesions on the leaves does not necessarily indicate the degree of susceptibility to root infection. For instance, primary lesions developed on six leaves of Red Durum and one developed on Monad, yet both are susceptible. The table also shows that the fungus caused a stunting of the plants. Twenty per cent of the inoculated rye plants were thus affected. Stunted plants form the second leaf below or at the ground line or a few millimeters above it. Typical lesions nearly always appear on the sheaths at or below the surface of the soil. The primary leaf was often rotted off completely at the ground line.

TABLE XI

Results of Inoculating Seeds of Wheat, Barley, Rye, and Oats with *H. sativum*

Variety	Number of plants		Primary lesions on leaves		Number of plants stunted		Dark colored basal sheaths	
	Inoculated	Check	Inoculated	Check	Inoculated	Check	Inoculated	Check
Wheat—Kota, C. I. 5878..	23	23	2	0	0	0	10	0
Acme, C. I. 5284.......	29	29	5	0	0	0	17	2
Mindum, C. I. 5296....	23	23	4	0	0	0	12	0
Kanred, C. I. 5146......	30	4*	7	0	1	0	11	0
Monad, C. I. 3320......	8	8	1	0	0	0	8	1
Marquis, C. I. 3641.....	16	16	9	0	1	0	10 .	0
Red Durum, Selection..	34	34	6	0	2	0	34	0
Red Cross, Selection....	13	13	3 .	0	1	0	†	
Red Wave, Selection....	18	18	2	0	1	0		
Illini Chief, Selection....	13	13	6 .	0	1	0		
Barley—Manchuria, Minn. No. 184	16	16	6	0	0	0	16	0
Rye—Minn. No. 2	20	20	8	0	5	0	8	0
Oats—Ligowa, Minn. . No. 281	2*	8	0	0	0	0	0	0

* Some plants were eaten by rats.
† A blank indicates that notes were not taken.

Measurements were made of individual plants of one variety of barley, one of rye, and six of wheat. The data are summarized in Table XII. It will be noticed that on an average the inoculated plants produced the first leaf nearer the ground line than did normal plants.

TABLE XII

Effect of Helminthosporium on Location of the First Leaf*

	Red Cross		Illini Chief		Red Wave		Monad		Kanred		Marquis		Rye		Barley	
	Inoculated	Check	Inoculated	Check	Inoculated	Check	Inoculated	Check	Inoculated	Check	Inoculated	Check	Inoculated	Check	Inoculated	Check
	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.
	1.8	1.9	0.8	1.9	1.6	2.9	1.7	2.0	1.5	1.4	0.9	1.7	1.4	2.0	2.7	1.7
	1.0	2.2	1.0	1.7	1.4	3.1	1.9	1.7	1.6	2.4	1.6	1.9	0.6	2.6	1.6	3.0
	1.5	1.8	1.0	1.5	1.0	2.5	2.1	2.4	2.6	1.6	1.7	2.8	0.0	2.7	1.9	2.2
	0.9	1.8	1.2	1.4	1.7	3.2	2.4	1.5	1.7	1.9	1.9	2.0	1.1	2.6	2.6	2.7
	1.5	1.4	1.7	1.8	1.5	2.3	1.0	1.8	2.6	1.4	2.4	2.4	0.0	1.8	1.8	2.6
	1.7	1.7	1.7	1.7	0.8	2.1	2.0	2.0	1.4†	2.8	1.9	0.8	2.0	2.4	2.7	2.7
	1.5	1.6	0.0	1.4	1.6	3.0	1.4	1.6			2.0	1.7	1.2	2.6	3.2	2.4
	0.7	2.0	1.9	1.8	0.0	2.7	1.3	1.7			1.5	2.8	0.7	2.4	2.0	2.8
	0.7	2.1	1.4	1.6	2.0	2.5					1.0	2.4	1.0	2.4	2.0	1.7
	0.1	2.0	1.8	1.5	2.0	1.7					2.2	3.0	1.5	1.8	2.0	2.6
	1.5	2.4	1.8	1.4	1.0	2.0					2.4	2.6	1.2	2.7	1.9	1.9
	1.7	2.3	1.1	1.3	0.8	2.0					0.0	1.7	0.5	2.8	1.8	1.6
	1.4†	1.6	1.4	1.4	2.0	2.1					1.7	1.8	0.0	2.4	1.7	2.0
			1.0	1.7	1.9	2.2					2.0	2.9	1.4	3.1	2.9	2.6
			1.7	1.7	1.6	1.8					1.4	2.9	1.6	2.7	1.6	2.8
			1.1	1.5	2.1	1.6					1.4	2.4	1.2	2.4	1.8	1.0
Total	16.0	24.8	20.6	25.3	23.0	37.7	13.8	14.7	11.4	11.5	26.0	35.8	15.4	39.4	34.2	36.3
Average height...	1.28	1.90	1.28	1.51	1.43	2.35	1.72	1.83	1.90	1.91	1.62	2.23	0.96	2.46	2.13	2.26

* Distance of first leaf from ground line.

† A blank indicates that no plants were inoculated.

On healthy rye plants first leaves were produced about two and a half centimeters from the ground line, while on infected rye plants they usually appeared less than one centimeter above the ground. The position of the leaf on Marquis and Red Wave was affected greatly by the presence of the fungus. There was scarcely any effect on Kanred, however, and only slight effect on barley. This undoubtedly is due to the fact that Manchuria, Minn. No. 184, the barley used, is resistant to *Helminthosporium sativum* (4).

On April 20 the tops of the wheat plants grown in Experiment II were cut off and discarded. The roots, however, were mixed with the soil. The soil and pots of the check series were autoclaved for four or five hours because a few of the check plants were infected with *Helminthosporium*. The same soil was then resown with the same varieties of wheat, using twenty seeds in each pot. The pots were all placed on a center bench in the greenhouse.

From Table XIII it will be seen that the greatest number of primary lesions appeared on Acme, Monad, and Kota. All plants grown in unsterilized soil developed brown basal sheaths, and nearly all were spindling and considerably shorter than the checks. The checks, with the exception of three plants, remained free from infection.

TABLE XIII

RESULT OF PLANTING WHEAT SEEDS IN INFECTED SOIL

Variety planted*	Variety planted†	No. of plants		Primary lesions on first leaf		No. of plants stunted	
		Inoculated	Check	Inoculated	Check	Inoculated	Check
Monad C. I. 3320	Kota C. I. 2151	18	19	3	0	4	0
Marquis C. I. 3641	Monad C. I. 2156	18	19	2	0	7	0
Red Durum Selection	Marquis C. I. 1239	17	19	1	0	1	0
Kota C. I. 5878	Kanred C. I. 5146	10	17	2	0	2	0
Kanred C. I. 5146	Mindum Minn. No. 470	20	20	1	0	2	0
Acme C. I. 5284	Red Durum C. I. 1446	14	20	0	0	2	0
Mindum C. I. 5296	Acme C. I. 1967	18	20	1	0	9	0

* Varieties of wheat first grown. Planted January 13, 1921.

† Succeeding varieties of wheat grown on the same soil and in corresponding pots. Planted March 20, 1921. Data taken from later planting.

Tables XIV and XV show the striking differences in height between plants grown in infected soil and those grown on autoclaved soil. (See Plate VII, Fig. 1.) Table XIV summarizes the height of plants eleven days after planting. Measurements were made from the ground line to the tip of the first leaf.

Kota was the most dwarfed of the seven varieties. Here the check plants were more than twice as high as the infected plants. Mindum appeared to be the most healthy, altho there was still a marked difference in size between the check and the infected plants.

Table XV gives the height of the plants eight days later. Measurements were made from the ground line to the tip of the highest leaf. It will be seen by referring to Tables XIV and XV that the effect of the fungus became more pronounced as the plants grew older. Marquis, however, recovered somewhat.

The appearance of the infected plants was similar to that described in the previous experiments. Subsequently the plants were grown almost to maturity. The striking difference between the check and the infected plants not only continued to exist, but became even more marked as the plants began to head. (See Plate VIII.)

In order to determine whether the fungus would attack the roots of grasses also, the following experiment was carried out: Eight four-inch pots of quartz sand were autoclaved for three hours under fifteen pounds pressure. The fungus was grown on sterilized wheat and this was mixed with the sand in four of the pots. To the control pots the same amount of steamed wheat was added, without the fungus. One check pot and one inoculated pot were sown with each of the following grasses: *Agropyron tenerum, Hordeum murinum, Bromus unioloides*, and *Lolium temulentum*. About the same number of seeds was used in the two pots for each species. Knop's nutrient solution was applied to all the pots after the seedlings were one or two inches high.

The results were very striking. The plants of all species were less vigorous in the inoculated pots than in the control pots. Nearly all the seedlings of *Agropyron tenerum* were killed (Plate III, Fig. 2.) *Lolium temulentum* was most resistant. Damping off was observed several times in the greenhouse on uninoculated plants of *Agropyron tenerum, A. caninum, Elymus canadensis, Hystrix patula*, and several others. Whenever cultures were made from such plants, *Helmintho-sporium sativum* was isolated.

TABLE XIV

Effect of Growing Wheat in Infected Soil on the Height of the Plant*

Kota		Monad		Marquis		Kanred		Mindum		Red Durum		Acme	
Inoculated	Check	Inoculated	Check	Inoculated	Check	Inoculated	Check	Inoculated	Check	Inoculated	Check	Inoculated	Check
cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.
4.0	12.0	8.7		10.5	11.9	5.6	11.3	11.0	15.0	9.8	11.0	7.0	10.0
6.5	11.8	7.5	13.0	9.2	12.5	3.9	8.8	11.8	12.2	4.0	10.5	7.7	13.0
6.0	12.2	8.5	12.0	11.5	12.7	7.5	11.2	12.9	14.7	11.1	11.4	8.5	11.7
7.2	12.5	11.5	12.5	8.7	12.5	7.5	7.7	7.6	13.6	10.6	13.5	10.5	11.4
6.0	12.2	5.7	12.0	7.5	12.5	8.5	6.4	11.0	13.8	8.5	5.4	6.0	12.5
7.5	11.9	8.7	14.0	5.0	12.0	6.8	8.8	12.0	15.0	10.1	11.5	8.9	14.1
3.5	13.0	7.0	11.5	11.0	12.6	2.2	7.4	10.5	14.6	11.0	9.4	9.0	12.2
6.0	11.9	6.4	12.5	11.0	12.9	4.7	10.4	8.5	14.2	12.0	11.4	8.0	12.5
11.0	12.4	8.0	11.5	11.0	11.8	3.5	8.7	9.5	13.8	12.5	13.2	8.6	11.8
6.0	9.0	8.5	11.5	9.0	13.2	9.2	9.8	10.7	14.7	6.5	14.9	8.6	12.2
6.0	12.5	8.7	13.7	6.5	12.8	†	9.5	10.5	13.0	11.5	11.6	9.8	14.7
5.5	12.0	7.2	11.7	7.5	11.9		9.0	3.6	13.3	10.8	10.6	9.2	12.4
5.4	12.7	8.0	9.0	10.9	13.5		10.9	10.2	13.5	9.7	13.5	8.0	11.0
7.6	13.5	9.0	12.8	8.0	13.4		4.5	11.4	14.6	11.9	12.4	9.6	11.3
11.2	12.2	4.3	11.2	12.5	12.0		5.5	10.7	15.2		10.5	5.5	14.1
6.5	12.8	11.0	12.7	10.5	13.2		8.0	11.2	13.4		7.5	7.9	12.9
11.6	13.4	8.2	12.4	9.0	13.0		10.0	12.7	12.5		8.6	10.3	12.5
6.5	12.7	6.2	12.5	9.0	13.0			8.7	14.7		11.0	9.5	10.9
	12.0		13.0					11.6	14.7		13.5		8.2
								11.9	15.1		9.5		12.3
Total 124.0	232.7	143.1	219.5	159.3	214.4	59.4	147.9	208.0	281.6	140.0	220.9	152.6	241.7
Average 6.88	12.25	7.95	12.19	9.37	12.61	5.94	8.70	10.40	14.08	10.0	11.04	8.47	12.08

* Measurements made eleven days after planting. For height eight days later see Table XV.
† A blank indicates that no plants were inoculated.

TABLE XV

Effect on Height of Plant of Growing Wheat in Infected Soil*

	Kota		Monad		Marquis		Kanred		Mindum		Red Durum		Acme	
	Inocu-lated	Check	Inocu-lated	Check	Inocu-lated	Check	Inocu-lated	Check	Inocu-lated	Check	Inocu-lated	Check	Inocu-lated	Check
	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.	cc.
	21.4	35.4	21.6	32.0	14.5	25.6	9.0	28.2	4.2	30.5	17.6	30.3	8.2	28.7
	19.9	31.8	10.4	30.3	14.7	27.1	12.2	22.0	8.0	31.4	11.0	16.7	14.3	17.8
	23.5	24.5	17.9	26.7	13.5	28.8	9.4	23.8	24.0	30.2	18.1	23.9	13.5	24.2
	13.4	32.0	10.0	26.8	9.0	24.2	16.0	17.4	24.6	26.7	15.4	22.5	17.9	29.2
	13.6	32.4	6.4	30.6	16.5	27.4	12.8	26.9	14.4	25.4	19.6	24.0	10.6	21.6
	12.2	36.2	13.2	21.6	12.6	25.5	15.7	27.5	15.4	22.0	19.7	24.4	11.9	30.6
	10.5	32.6	14.6	24.0	14.4	26.5	19.0	26.5	23.7	29.4	16.0	25.2	8.6	35.8
	18.1	31.1	15.5	25.7	16.7	25.4	14.4	28.1	15.5	30.4	14.5	24.1	14.0	31.0
	11.2	30.2	13.7	28.4	18.0	24.2	17.3	29.4	17.8	32.3	19.6	24.1	15.2	22.5
	12.0	23.0	14.4	19.4	15.5	26.3	9.6	20.4	15.8	30.2	18.5	23.9	13.1	30.3
	15.1	33.0	9.7	25.0	16.3	26.9	14.7	15.8	17.0	24.5	18.0	24.2	14.2	31.4
	9.0	35.0	20.3	29.0	17.6	26.5	17.9 †	23.0	11.7	26.4	17.0	22.6	9.5	24.9
	9.5	35.2	14.6	22.6	15.0	24.2		18.3	23.0	23.5	16.1	20.6	7.0	48.0
	9.6	34.8	12.4	34.0	18.0	28.9		20.0	22.8	31.2		29.0	9.6	25.6
	10.9	28.5	14.5	26.9	16.4	25.4		22.2	21.7	25.0		23.6	15.3	21.5
	14.4	23.0	12.3	28.5	14.7	26.1		16.5	25.4	28.3		25.0	14.6	29.2
	19.5	32.0	15.6	32.8	16.5	23.5		15.6	21.4	53.2		23.7	15.8	23.8
	17.3	31.0	21.2	19.1					21.5	29.0		26.5	14.0	25.7
									22.0	24.1		31.9		35.9
										29.5				32.3
Total	261.1	561.7	258.3	483.4	259.9	442.5	168.0	381.6	349.9	563.2	221.1	460.2	228.5	550.0
Average	12.5	31.1	14.4	26.8	15.2	26.2	14.0	22.4	18.4	28.1	17.0	24.5	12.8	27.5

* Measurements made nineteen days after planting. For height eight days earlier see Table XIV.

† A blank indicates that no plants were inoculated.

NATURALLY INFESTED SOIL

In order to determine whether root rot and stunting of susceptible varieties of wheat and barley would occur when clean seed was sown in naturally infested soil, the following experiments were carried out in the greenhouse during the winter of 1921-22. Soil was taken from a field which had grown barley in 1920 and 1921, and which previous to that time had produced truck crops and grasses. In both of the years in which barley was grown, the plants were sprayed with a suspension of spores, and in 1921 were severely infected with root-rot. The soil was placed in twenty eight-inch pots. Ten of these were autoclaved for three hours under a pressure of fifteen pounds.

The following varieties were used: Manchuria barley, Minn. No. 184, and Arequipa selection; Marquis wheat, C. I. 3641; Monad durum, C. I. 3320; and Victory oats, Minn. No. 514. Fifteen seeds which had been disinfected in the regular manner were sown in each pot. Two series were carried out, in each of which one pot of sterilized and one of unsterilized soil were used for each of the five varieties. The positions of the pots were interchanged every seven to ten days. The final notes on the comparative development of the plants were taken when they were beginning to head. Measurements were made from the ground line to the tip of the highest leaf. Table XVI summarizes the data obtained from this experiment. In both series Marquis and Monad wheat and Arequipa barley in unsterilized soil became very much stunted. For instance, the check plants of Marquis in Series 1 were, on the average, more than twenty-nine centimeters higher than those in non-autoclaved soil. Table XVI shows this marked difference, Manchuria barley, which is resistant in the field, appeared resistant also in this experiment, altho the height of the check plants should be greater than expressed in the table, as three or four plants in the check pots became severely infected from seed infections and did not develop normally. The average differences in the two series of oats are insignificant. The infected plants of Marquis produced on the average two or three culms, while the control plants developed only one. This experiment and field observations of the plants grown in the plots from which this soil was taken, indicate that soil harbors the pathogene. The facts that Manchuria grew about equally well on sterilized and non-sterilized soil and that oats grew slightly better in the control pots, indicate that the effects noted were not due to toxins. Moreover, the soil had not grown cereals for ten years and it is not probable that barley could excrete enough toxins in one year to stunt the plants. *Helminthosporium sativum* is apparently an important agent in making soils unproductive.

TABLE XVI

Effect of Growing Wheat, Barley, and Oats on Naturally Infected Soil

Variety	Series 1				Series 2				Average difference in height of plants	
	Number of plants		Average height of plants		Number of plants		Average height of plants		Series 1	Series 2
	Infected soil	Check	Infected soil	check	Infected soil	Check	Infected soil	Check		
			c.m.	c.m.			c.m.	c.m.	c.m.	c.m.
Wheat										
Marquis, C. I. 3641	10	11	46.60	76.18	10	11	52.70	76.54	+29.58*	+23.84
Monad, C. I. 3320	12	12	51.41	71.41	13	12	65.84	72.08	+20.00	+6.24
Barley										
Arequipa Selection	11	13	48.63	57.61	11	15	50.72	57.73	+8.98	+7.01
Manchuria, Minn. No. 184	13	14	50.07	54.25	10	15	59.40	55.46	+4.18	−3.94
Oats										
Victory, Minn. No. 514	14	11	66.27	63.85	13	13	78.61	81.07	−2.42	+2.36

* The plus sign indicates an increase and the minus sign a decrease in the height of the check plants.

INFECTION RESULTING FROM DISEASED SEED

An equal number of black-tipped and badly discolored seeds of wheat and barley were disinfected and planted in sterilized quartz sand. Duplicate pots were planted. Most of the wheat and barley plants developed from diseased seeds were much less vigorous than those produced from clean seeds. When the seedlings were about two weeks old the sand was carefully washed away from the roots. It was found that the fungus was fruiting luxuriantly on many of the infected seeds. Some of the seeds had been attacked so rapidly and so severely that they failed to germinate. Others had germinated but the shoots were killed before reaching the surface. Both roots and stems were sometimes destroyed. (See Plate II.) Many of the plants that survived were stunted and weak. There were brown lesions on the roots and foot, and on the basal sheaths of the plants developed from the infected seeds. Usually the roots just below the crown were most severely infected. The length of the diseased areas varied from a fraction of a centimeter to three centimeters or more. The difference in root development also was very marked. The roots were not nearly so numerous or so vigorous as those on plants from healthy seed. This experiment was repeated and very similar results were obtained. Infected seeds of *Hordeum murinum* were sown in sterile sand and the results were similar to those described for wheat and barley.

The fungus was isolated repeatedly from seeds of many varieties of wheat, barley, and rye, and from several species of grasses. Samples of Monad wheat from North Dakota showed almost 100 per cent infection when the seeds were plated out on agar. From 50 to 75 per cent of infected seeds is not uncommon for many varieties of wheat and barley at University Farm.

Louise J. Stakman (9) found that when infected seeds were sown in the field they germinated poorly, the seedlings were weak and spindling, and there was a characteristic foot-rot and distinct rosetting due to excessive stooling.

VITALITY OF THE FUNGUS

The conditions under which Helminthosporium overwinters have been imperfectly known. Investigations were undertaken to find out whether the mycelium and the spores both overwinter. In the fall of 1921, infected wheat and barley plants were left unprotected in the field, and some were stored in a dry basement. Later in the fall several bottles containing agar or sterilized wheat straw were inoculated with Form I of *Helminthosporium sativum*. When the substratum was fairly well covered with spores, they were treated in the following

manner. Two bottles containing agar and two containing wheat straw were covered with from five to seven centimeters of water; four similar cultures were covered with five to ten centimeters of sand. In each case one set was placed outdoors in the fall of 1921 and the other was kept in the laboratory at room temperature. Isolations were made on April 16, 1922. The results given in Table XVII indicate that the fungus does overwinter in the field unprotected and also when imbedded in ice or covered with moist sand.

Hanging drop cultures were made from spores kept outside over winter on agar and covered with moist sand or water. No germination was obtained. These experiments indicate that spores do not overwinter under moist conditions, but that the mycelium survives.

In the laboratory the spores remained viable for a long period. Thus spores kept covered with moist sand for more than five months germinated readily. Likewise spores from a transfer twenty-three months old kept at ordinary room temperature germinated when placed in drops of water.

The data in Table XVII show that the fungus retains its viability in the laboratory under varying conditions for a considerable length of time. Numerous plantings from diseased seed kept indoors proved that the mycelium may live for several years; in fact, the organism was isolated during the spring of 1921 from seed of the 1914 crop. Usually, however, the hyphae in such seed are dead. An unsuccessful attempt also was made to isolate the fungus from badly diseased leaves which had been kept in the laboratory since 1915, i.e., for a period of six and a half years.

TABLE XVII

RESULTS OF OVERWINTERING STUDIES ON *Helminthosporium sativum* 1921–1922

Substratum	Treatment	Date begun	Results* Outside†	Results* Laboratory
Potato dextrose agar	Covered with from 5 to 10 centimeters of moist sand	11-14-21	Positive	Positive
Potato dextrose agar	Covered with from 5 to 7 centimeters of water	11-14-21	Positive	Positive
Wheat straw	Covered with from 5 to 10 centimeters of moist sand	12- 2-21	Positive	Positive
Wheat straw	Covered with from 5 to 7 centimeters of water	12- 2-21	Positive	Positive
Wheat straw	Covered with from 5 to 10 centimeters of black loam	12- 2-21	Positive	?
Wheat straw, roots, and glumes	Left in field and stored in basement	Fall, 1921	Positive	Positive
Barley straw, kernels, and awns	Left in field and stored in basement	Fall, 1921	Positive	Positive

* Cultured April 16, 1922.

† Part of each set was placed in the laboratory and part outside.

SOURCE OF INFECTION

The initial infections in the field and greenhouse come from seed or from soil. The fungus, as already indicated, was isolated more than 200 times from discolored seeds of more than one hundred species and varieties of wheat, barley, rye, and grasses. Many seeds of barley and durum wheat were planted on agar and colonies of Helminthosporium developed on from 85 to 100 per cent of the seeds of some varieties. When black-pointed seed of barley and wheat were germinated on sterile blotting paper or planted in sterilized quartz sand, Helminthosporium often grew from them. Miss Evans (2) obtained similar results with wheat.

Plants grown from such discolored seed nearly always produce a foot- and root-rot from which *Helminthosporium sativum* was repeatedly isolated, while plants grown from clean seeds remained healthy. Waterhouse (11) observed the hyphae of Helminthosporium in young plantlets of wheat, the infection having resulted from diseased seed. The disease was reproduced in the greenhouse from soil obtained from infected areas in the field. Stevens (10) obtained similar results.

The above experiments on overwintering demonstrate that the fungus overwinters in the field on old straw, roots, and seed. In fields of wheat which had been severely infected with seedling blight and root-rot in 1919, the disease was again destructive in 1921. It is hard to correlate definitely the seriousness of the disease with crop history, because the amount of injury depends also on other factors, such as temperature, moisture, etc.

Secondary infection results from a variety of sources. In the spring the fungus has been observed to fruit on the nodes of plants of the previous season. The fungus also sporulates freely on primary lesions. The spores are then distributed by such agents as rain, water, and wind, the last undoubtedly being the chief factor. In the recent rust epidemiology studies made by the Office of Cereal Investigations of the United States Department of Agriculture (8) during the spring and summer of 1921, numerous spores of Helminthosporium were caught by spore traps at elevations up to ten thousand feet.

Once the fungus has sporulated on the plants, repeated inoculations and infection may occur as in cereal rusts, potato late blight, and similar diseases. It was found by experimentation that the mycelium and spores remained alive in the laboratory after having been buried in coarse moist sand for more than five months. The longevity of the spores and mycelium probably plays an important part in producing an epidemic of this disease.

The effect of wild grasses on increasing secondary infections of cereals is important, as a large number of the common grasses are susceptible; and as the fungus overwinters on their remains they very likely aid greatly in the dissemination of the disease.

CONTROL

The problem of controlling the disease has not been sufficiently investigated, and the control measures recommended at the present time are altogether inadequate. F. Kolpin Ravn (7) demonstrated clearly that Jensen's modified hot water treatment eliminated *Helminthosporium teres* and *H. gramineum* from the seeds. Louise J. Stakman (9) states that long-time soaking in formaldehyde reduced the amount of *Helminthosporium sativum*. These treatments, however, do not eliminate secondary or soil infections, and these are probably the most important. The following control measures suggest themselves in the light of the facts brought out in this investigation: (1) Planting clean seed; (2) Good cultural methods; (3) Rotation of crops; (4) Use of existing resistant varieties and the development of additional resistant varieties with more desirable agronomic characters.

Since it has been shown definitely that the disease is seed-borne and that infected seeds often produce diseased plants, clean seed is essential. That sowing grain late in the spring favors the development of root-rots is indicated by the fact that the optimum temperature for the pathogene is relatively high. It does not thrive nearly so well when the soil is cool (40° to 60° F.), whereas wheat, barley, and rye seedlings develop a better root system and are more vigorous at these temperatures than at the higher temperatures which are more favorable for the rapid growth of the fungus. Therefore if susceptible grains are grown they should be sown as early as possible in the spring. Observations at University Farm indicate that root-rots and seedling blight are more prevalent in fields which have been cropped continuously to wheat than in those on which rotation has been practiced. As the disease lives over in the soil or on the remains of susceptible plants, a rotation which includes an immune or highly resistant crop, such as corn, clover, timothy, or vegetables is beneficial in reducing the disease. Altho good cultural methods and the use of clean seed may reduce the amount of damage and in certain years may control the disease, the most promising method of control is the development of resistant varieties. Manchuria barley, Minn. No. 184, was resistant to several forms of *Helminthosporium sativum* in Minnesota. Coöperative breeding work between the Division of Plant Pathology and Botany and the plant breeding section has been under

way for some time at University Farm (4). Preliminary varietal tests were made with fifty varieties of wheat and they were partially checked in the greenhouse under controlled conditions. The results indicate that resistant varieties may be obtained. For example, Kanred wheat appears to be highly resistant to root-rot caused by Form I, while Marquis is susceptible to root-rot caused by this biologic form, but is fairly resistant to seed blight and head blight.

More detailed studies of the factors that favor the development and spread of the disease, the longevity of the fungus in the soil, as well as the number of biologic forms which occur, must be carried on to insure the best results in selecting and breeding resistant varieties.

DISCUSSION AND CONCLUSIONS

It has been known for some time that *Helminthosporium sativum* caused the spot-blotch of barley, but it has not been known until recently that the same fungus also can cause root- and foot-rots, discoloration of the nodes, leaf spots, glume spots, and discoloration and shriveling of the kernels of the common small grains and a great many wild grasses.

Since Bolley first called attention to the destructiveness of the Fungi Imperfecti to cereals, considerable work has been done in attempting to ascertain the exact part played by certain of them in reducing yields of small grains. There seems to be no question whatever but that *H. sativum* is one of the most destructive of these fungi.

The losses caused by *H. sativum* are undoubtedly considerable. It appears that in Minnesota, at least, this organism is the cause of most of the root-rotting of wheat, barley, and rye. In some years the disease is very destructive. At times the damage is not conspicuous since only isolated individuals are killed, but at other times the plants are stunted or killed in definite, more or less circular areas, which are very striking. In either case, the aggregate damage may be considerable. Experimental work done at University Farm indicates clearly that losses may be very great when the soil is constantly cropped to susceptible varieties of cereals.

Not only is *H. sativum* a virulent parasite in various parts of the spring wheat region, but it apparently is quite widely distributed in the United States, having been isolated from grains and grasses from widely separated regions in this country. It is also known to occur in various regions of Canada, in Mexico, in the Argentine, and in Australia. Apparently it is not yet known in Europe. It is quite possible, however, that it occurs but that the damage which it does is confused with the damage caused by various other root- and foot-rotting fungi.

It has generally been considered that *Helminthosporium sativum* is a group species. Several investigators have noticed that the fungus varies considerably not only in cultural characters on different media but in spore size. This can be explained partially at least by the existence of several biologic forms which differ from each other very markedly in cultural characters. The morphology of the spores of the different forms varies slightly and there are some differences in their parasitic behavior. However, the principal difference is in their cultural characters. Each of these biologic forms is constant when grown under the same environmental conditions, but cultural characters and morphology of spores are profoundly influenced by changes in environmental conditions. The effect of the medium on which a form is grown, and the effect of temperature is sometimes so great as to make it practically impossible to distinguish the form. The consistent difference between different forms under known conditions and extreme variability of each individual form are very significant. This variability simply emphasizes the fact that extreme caution is necessary in determining species of Helminthosporium and other similar fungi which may vary quite as much as does this one. Descriptions of such organisms can be given only after careful studies have been made under known environmental conditions.

There are some indications that there are still more forms than those which have been discovered so far. It is quite possible that they may differ from each other pathogenically more sharply than do those now known. If this should be true, then the existence of these forms will complicate the problem of procuring varieties of cereals resistant to this organism.

The pathogenicity of *Helminthosporium sativum* was studied extensively. The host range is extremely wide. Not only does the organism attack wheat, barley, and rye but it also attacks about eighty-three species of wild grasses belonging to 37 different genera. This was demonstrated by making isolations from a great many wild grasses, by inoculation experiments in the field, and by carefully controlled inoculation experiments in the greenhouse. The fact that the organism can attack so many different hosts, under such wide range of conditions, makes its control extremely difficult.

The pathogene overwinters very readily in Minnesota in soil, in seed, and in dead-plant parts. It has been shown that hyphae may remain in seeds for several years. Since the organism also is a faculative saphrophyte and can grow on dead or dying plant remains and even in the soil, the number of spores is very large. A very high percentage of wheat seed is likely to be infected with the organism. Many primary infections therefore probably come from seed. It

has been shown, however, that the use of clean seed in infested soil does not protect plants from infection. Many experiments were made which indicate that primary infections may result from the spores or mycelium in the soil. Secondary infections are very numerous. They are caused principally by wind-blown spores. That the spores are very numerous and widespread is indicated by the fact that they have been caught by spore-traps in airplanes at altitudes up to 10,000 feet.

It is quite obvious that control measures are difficult. The use of clean seed, when it can be procured, is of course recommended. Furthermore, the seed should be sown on land which has not grown an infected crop for several years. The hyphae inside the seed are not killed by the ordinary treatment such as is given for the prevention of covered smuts. It is sometimes difficult to kill the intraseminal mycelium even by special methods. Soil can be kept reasonably free from the pathogene by practicing a proper system of rotation. The use of corn, potatoes, clover, or oats in the rotation would be highly beneficial, since none of these crops is susceptible to the disease. However, the wild weed grasses are practically always present. If our cultural practices included killing these grasses, it would assist greatly in controlling two of our very serious diseases, namely, stem rust and the Helminthosporium disease. Even tho clean seed is available and is sown on reasonably clean soil, there is always the danger of infection by means of wind-blown spores which have been developed on susceptible wild grasses. The most promising method of control is the development of resistant varieties. Considerable progress already has been made in the development of resistant types of barley, and there are indications that there are sufficient differences in the susceptibility of varieties of wheat to make it possible to select or breed desirable resistant varieties.

SUMMARY

1. *Helminthosporium sativum* Pammel, King, and Bakke, which causes a serious disease of wheat, barley, and rye in Minnesota, appears to be very widely distributed, since inoculations with cultures obtained from different regions of the United States, Canada, Argentina, and Australia produced typical spot blotch on barley. The same organism was also isolated from wheat grown in Mexico.

2. *H. sativum* causes leaf spots, root-rots, foot-rots, seedling blight, head blight, and badly discolored seeds of wheat, barley, and rye, and many grasses. The organism also causes stunting of wheat, barley, and rye and excessive stooling of wheat and barley.

3. No parts of the susceptible plant are immune. Roots, stems, leaves, glumes, awns, and seeds may be attacked. Plants may be highly resistant, or even immune in the early stage of development, but later the same plants may become very susceptible.

4. Hundreds of isolations were made from infected plants found not only in Minnesota and adjoining states but also in various regions of the United States and other countries. The fungus was isolated from many naturally infected cereals and grasses, including several varieties of rye, 20 varieties of barley, 70 varieties of wheat, and 32 species of common grasses.

5. Biologic specialization occurs in *Helminthosporium sativum*. At least four forms have been found. These forms differ physiologically as is indicated by the rate and character of their growth on the same and different media and by the fact that they produce different degrees of infection on the same cereals and grasses.

6. The spores of the four biologic forms of *H. sativum* differ slightly in width and length and in the number of septa, as do also spores of a single form produced under different conditions.

7. Extreme variation of an individual biologic form of *H. sativum* under different conditions, and of different biologic forms under the same conditions makes it almost impossible to give a technical description of the species which would be generally applicable. A large number of spores must be measured to obtain reliable results, and any given dimension of spores is applicable only to a specific set of conditions.

8. *Helminthosporium sativum* has a very wide host range. Of the 134 species of cereals and grasses inoculated in the greenhouse with Form I, 98 became infected. Fifty-eight of these were susceptible and 40 were somewhat resistant. The remaining 36 appeared to be immune. Of the 66 species inoculated in the field, 57 became infected.

9. Wheat, barley, and rye are susceptible. The various species of oats and corn inoculated were practically all immune. The common grasses which are very susceptible are: *Setaria viridis, Hystrix patula, Chloris verticillata*, and various species of *Agropyron, Bromus, Elymus, Festuca, Hordeum*, and *Lolium*; those which are immune or extremely resistant are: *Phleum pratense, Arrhenatherum elatius, Alopecurus pratensis, Koeleria cristata*, and species of *Phalaris, Poa*, and *Agrostis*.

10. Field and greenhouse experiments with Form I proved that Marquis, Monad, and Red Durum wheats were extremely susceptible to root infection, while Kanred was resistant. Of the barleys, Lion, Bay Brewing, and Arequipa were very susceptible, while Manchuria,

Minn. No. 184, was quite resistant. Oats were either immune or highly resistant, while rye was slightly susceptible.

11. Stunting, excessive stooling, and spindling growth of susceptible plants were produced in the greenhouse under controlled conditions, as a result of artificial inoculation with *H. sativum*. This fungus also causes a shortening of the distance between the ground-line and the base of the first leaf of infected plants.

12. Typical foot- and root-rot developed on wheat and barley when planted in infected soil in the greenhouse. The plants were spindling and dwarfed, and seedling blight was common. *H. sativum* was isolated from the diseased plants. Similar results were obtained by planting diseased seeds in clean soil.

13. *Helminthosporium sativum* overwinters as mycelium in the seed and on plant remains in the field. The mycelium has been shown to remain viable in seed for several years. Spores kept over winter outdoors in moist sand did not germinate in the spring, while spores under similar treatment in the laboratory were viable at the end of five months. Spores produced on a culture medium germinated freely at the end of twenty-three months. The mycelium also remained alive for many months when kept under varying conditions.

14. Initial infections in the field and greenhouse are due to seed infection and soil infestation. Secondary infections result from spores produced on primary lesions on cereals, from infected plants of the previous season, and from many diseased common grasses.

15. The fungus grows and sporulates not only on living plants, but also on dead and decaying plant parts.

16. The disease is extremely hard to control. Proper rotation and clean seed will reduce the prevalence of the disease but will not eliminate it. The use of resistant varieties seems to be the most promising means of control.

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EXPLANATION OF PLATES

Plate I.

Badly infected Arequipa barley. Note numerous lesions. No heads developed on account of severe root infection. Photographed at harvest time. (Grown on Plant Pathology and Plant Breeding plot, 1921.)

Plate II.

Different degrees of infection on wheat, grown from black-tipped kernels in sterilized sand. *H. sativum* fruiting on seeds. Healthy plant on extreme right.

Plate III.

Fig. 1. Badly infected barley hybrid. Note excessive stooling. (Grown on Plant Pathology and Plant Breeding plot.)

Fig. 2. Effect of growing grasses in sand inoculated with *H. sativum*. From left to right.

A. *Agropyron tenerum:*
> Inoculated
> Check

B. *Hordeum murinum:*
> Inoculated
> Check

Plate IV.

Fig. 1. Black-tipped seeds of wheat sown on potato dextrose agar. Pure cultures of *H. sativum* developed from six and *Alternaria sp.* from the seventh.

Fig. 2. Photomicrograph of spores of *Helminthosporium sativum* developed on moist heads of wheat.

Fig. 3. Germinating spores.

Plate V.

Four biologic forms, I, II, III, and IV, of *H. sativum* on green bean agar. Compare with Plate VI.

Plate VI.

Four biologic forms, I, II, III, and IV, of *H. sativum* on one per cent potato dextrose agar. Compare with Plate V.

Plate VII.

Fig. 1. Second crop of wheat grown on soil previously infested with *H. sativum*. From left to right.

A. Monad:
> Sterilized soil
> Infested soil

B. Acme:
> Sterilized soil
> Infested soil

C. Kota:
> Sterilized soil
> Infested soil

Fig. 2. Effect of soil inoculated with *H. Sativum* on wheat. From left to right.
> A. Kota:
> > Check
> > Inoculated
> B. Red Durum:
> > Check
> > Inoculated
> C. Marquis
> > Check
> > Inoculated

Plate VIII.
> Second crop of wheat grown on soil previously infested with *H. sativum*. Same plants as in Plate VII, Fig. I, except that Marquis is substituted for Monad. From left to right
>
> > A. Acme:
> > > Infested soil
> > > Sterilized soil
> >
> > B. Marquis:
> > > Infested soil
> > > Sterilized soil
> >
> > C. Kota:
> > > Infested soil
> > > Sterilized soil

Plate IX.
> Different degrees of infection on two-rowed barley grown on peat soil in 1921. All the plants are the same age.

Plate X.
> Result of growing wheat, barley, and oats on soil naturally infested with *H. sativum*. From left to right.
>
> > A. Marquis wheat:
> > > Infested soil
> > > Sterilized soil
> >
> > B. Arequipa barley:
> > > Infested soil
> > > Sterilized soil
> >
> > C. Manchuria barley:
> > > Infested soil
> > > Sterilized soil
> >
> > D. Victory oats:
> > > Infested soil
> > > Sterilized soil

PLATE I

PLATE II

FIGURE 1

FIGURE 2
PLATE III
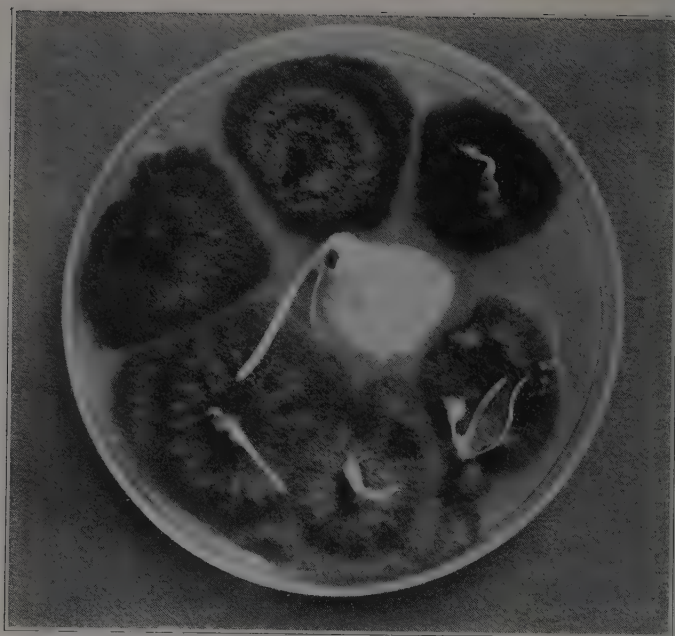
FIGURE 1

FIGURE 2
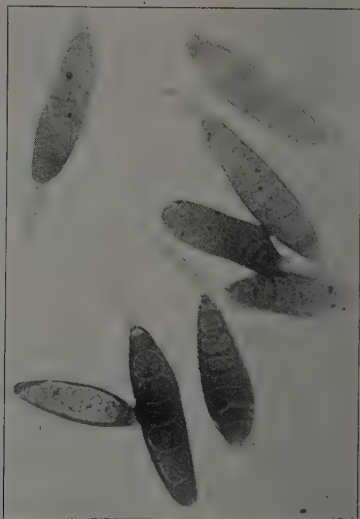
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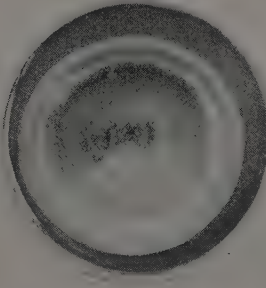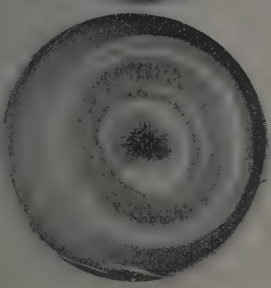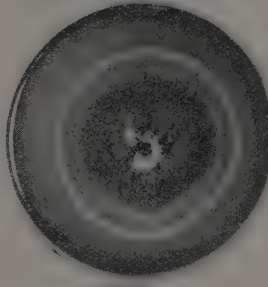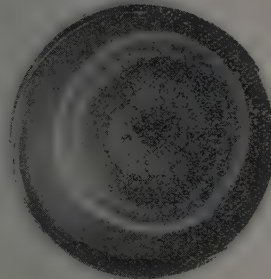
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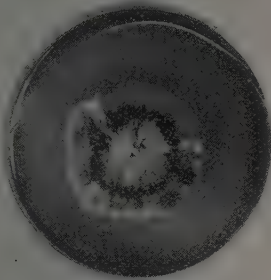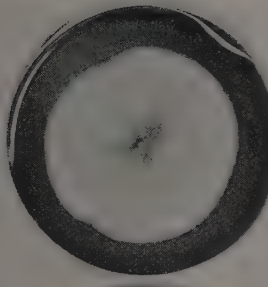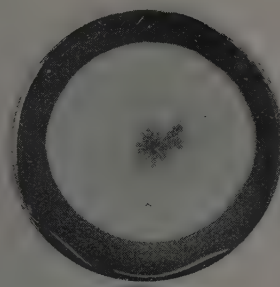
PLATE V

PLATE VI

I II III IV
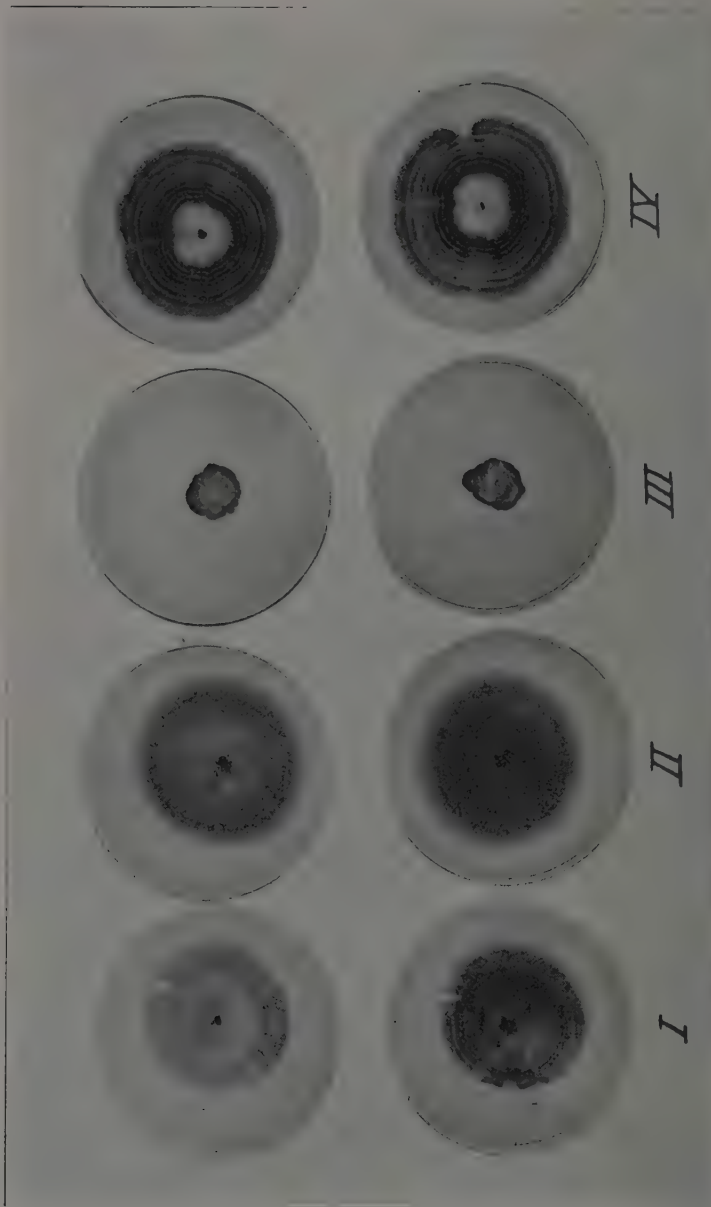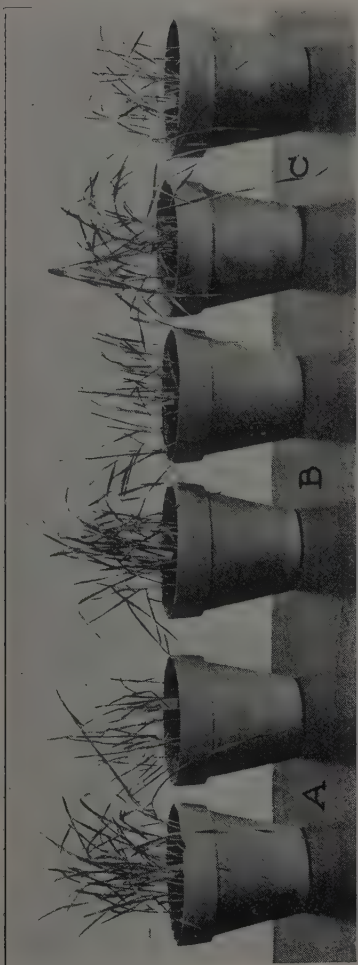
FIGURE 1

FIGURE 2
PLATE VII

PLATE VIII
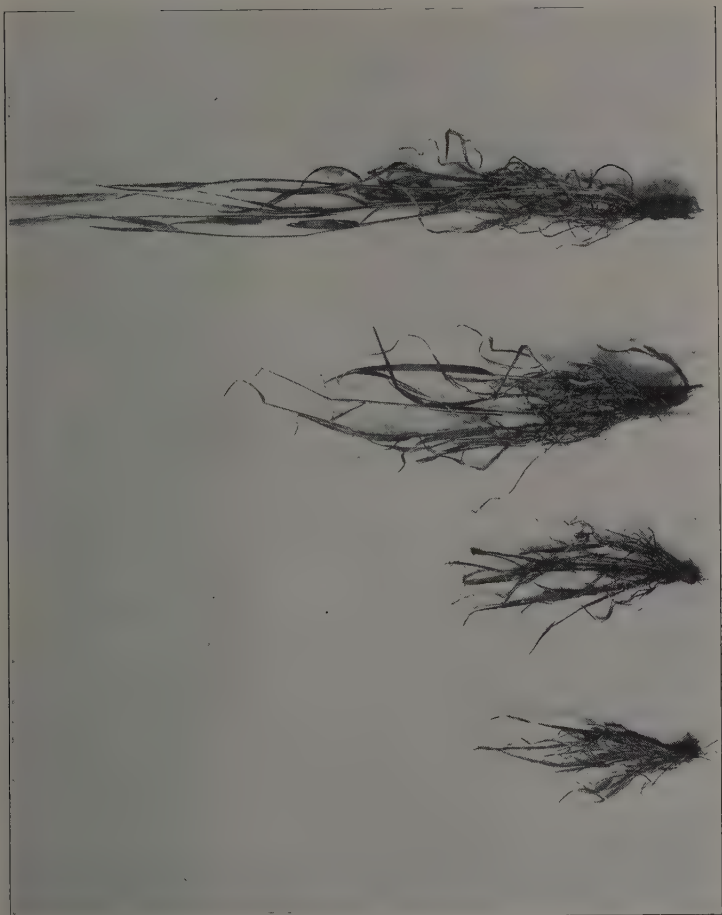
PLATE IX

PLATE X.

The University of Minnesota
Agricultural Experiment Station

Studies in the Physical Ecology
of the Noctuidae

By WILLIAM C. COOK
Division of Entomology and Economic Zoology

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Studies in the Physical Ecology
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CONTENTS

ILLUSTRATIONS

STUDIES IN THE PHYSICAL ECOLOGY OF THE NOCTUIDAE

By W. C. Cook

INTRODUCTION

This paper gives the results of an attempt to determine the effects of the various meteorological factors on the distribution, seasonal abundance, and activity of certain species of the insect family Noctuidae, which are commonly classed as cutworms and army worms. As yet the studies include but few species, but the results so far obtained seem of fundamental importance, and the methods used, altho somewhat novel to entomologists, are applicable to the solution of many similar economic problems.

DEFINITIONS OF TERMS

Physical ecology may be defined as the study of physical factors in their relation to the ecology of a species. Such factors are light, heat, and moisture as opposed to associational factors such as parasites, or chemical factors such as food relations. The study of these physical factors under field conditions comes within the realm of meteorology, and the factors themselves fall into two general classes, weather and climate. Prof. J. Warren Smith ('20, p. 1)[1] makes the following comparison of these groups:

"Weather is the condition of the atmosphere at a definite time. It includes all the phenomena of the air that surrounds us, such as pressure, temperature, moisture, wind, and the like.

"Climate deals with the averages and the extremes of the weather that prevail at any place. Thus it will be seen that weather relates to time and climate to location."

LITERATURE

Most of the previous work on insect forms has been confined to laboratory experiments under controlled conditions or to the drawing of general conclusions from a superficial study of field data, without subjecting the data to any form of mathematical analysis. This is the case in the early development of any branch of science, the qualitative form preceding the quantitative. Our entire knowledge of quantitative physical ecology may be said to consist of a few definite laws of growth deduced from laboratory experiments, and a few broad generalizations on the effects of climate on animal and plant distribu-

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[1] Dates in parentheses refer to titles in the list of literature cited at the end of the paper.

tion and activity. Some of the more important of these deductions are worthy of mention in connection with this specific problem.

Working under controlled laboratory conditions, Sanderson and Peairs ('13) determined that the effect of temperature upon insect growth might be represented by a rectangular hyperbola of the formula $XY=A^2$, A being a constant, called by them the thermal constant, X being the temperature, and Y being the time of development. By plotting X against $\frac{1}{y}$, the plot becomes a straight line which intersects the temperature axis at the point $\frac{1}{y}=0$, or point of no growth, which they called the developmental zero. The quantity $\frac{1}{y}$ they have termed the index of development, and it represents the part of total growth accomplished in one day. In most cases in which this method of plotting was used, it has been found that the relations outlined above hold true for the portion of the temperature range which is approximated under field conditions, and that the developmental zero found mathematically is a very close approximation to the point of dormancy under field conditions.

W. D. Pierce ('16) showed that the effect of temperature combined with humidity was to change the developmental zero of Sanderson to an elliptical curve whose foci were the optimum condition, and that Sanderson's curve of growth was a zone inside of this ellipse. Any cross-section of this zone, parallel to the humidity axis, gave a hyperbolic temperature curve, as before.

Studying the distributional data obtained by the United States Biological Survey, C. H. Merriam ('98) formulated a general law of animal and plant distribution, as follows ('98, p. 54).

"Investigations conducted by the Biological Survey have shown that the northward distribution of terrestrial animals and plants is governed by the sum of the positive or effective temperatures for the entire season of growth and reproduction, and that the southward distribution is governed by the mean temperature of a brief period during the hottest part of the year."

By the term "effective temperatures" is meant all temperatures above 43° F, which was then regarded as a general developmental zero.

Sanderson ('08) showed quite conclusively that the northward distribution of some insect species was limited, not by the sum of effective temperatures, but by the minimum winter temperature, and recommended the inclusion of this factor in Merriam's law.

A. D. Hopkins ('18) has formulated an empirical bioclimatic law, stating that in general, in temperate North America, the time of occurrence of any given periodic event in life activity becomes later in the spring and earlier in the fall as we progress northward, eastward,

and upward. The general rate of change is four days for each degree of latitude, each five degrees of longitude, and each four hundred feet of altitude.

The bioclimatic law does not represent conditions on the Pacific Coast, and there is a gradually decreasing error in its application until the region well east of the Rocky Mountains is reached. As the author of the law has stated, it is a purely empirical deduction from field observations, and apparently the basis of the law is the gradual change from marine to continental climate progressing from east to west as we go inland. Possibly a restatement of the law, based upon distance from the ocean rather than upon westward progression, would give smaller errors in the western part of the range.

Aside from the general problem of the effects of climate upon animal distribution, efforts have been made to connect certain climatic conditions with specific insect outbreaks. No attempt will be made here to include all the work done on this problem, but a few abstracts will be given to show the general character of the work.

One of the early attempts in this direction was the hypothesis advanced by Asa Fitch ('60) to account for army worm outbreaks. It is quoted in full ('60, p. 121).

". . . more briefly expressed, my view is this—a dry season and dry swamps multiplies this insect. And when it is thus multiplied, a wet season and overflowed swamps drives it out from its lurking place in flocks, alighting here and there over the country. But on being thus rusticated, it finds our arable lands too dry for it and immediately on maturing and getting its wings again, it flies back to the swamps, whereby it happens that we see no more of it."

This view was also supported by C. V. Riley ('70, '76), and shows that even in this early stage in the development of entomology, it was recognized that climatic factors might explain insect outbreaks.

Charles G. Barrett ('82) gives notes on the distribution of various Noctuid species in an English district following two types of winter conditions, and concludes that the abundance or rarity of native species is largely determined by climatic conditions. Four successive mild winters made certain species, which were ordinarily common, very rare, and other ordinarily rare species quite common. Following these winters came three severe winters, after which the normal balance was restored.

In considering the relation of precipitation to insect distribution, Criddle ('17) cited the Rocky Mountain Locust as an example of an insect which is increased greatly during dry seasons, and also states that in Manitoba the Hessian Fly is checked by a drouth sufficient to ripen the wheat prematurely. He shows that the combination of light

snowfall and low winter temperature has been fatal to the Colorado potato beetle in most parts of Manitoba, and considers that it will probably never be a major pest in that region.

In the realm of plant ecology, especially in the study of the economic crop plants, there is a rapidly increasing body of work upon the mathematical study and analysis of climatic relations. J. Warren Smith ('20) brings together the principal work relating to the effects of climate upon crops, using statistical methods for the more or less exact definition of critical growth periods. In many cases it is now possible to predict the amount of a given crop on a certain area if the weather conditions during these critical periods are known. This work is very valuable and suggestive, and the methods used there have been adopted in part in this paper.

LINES OF STUDY PURSUED

This paper is based upon studies along three distinct but related lines, laboratory experiments upon temperature and soil moisture relations, attempts to correlate these results with the conditions surrounding outbreaks of three species in the field, and a statistical interpretation of data relative to the effects of weather conditions on moth flight. The work was begun at University Farm, St. Paul, in 1919, in connection with cutworm investigations undertaken for the Minnesota Agricultural Experiment Station, and carried through two seasons, during which time all the original data relating to Minnesota conditions were secured. During 1921 the work was carried on in Montana in connection with investigations of the life history and control of the Pale Western cutworm (*Porosagrotis orthogonia* Morr.) for the Montana Agricultural Experiment Station, and all the original data relating to Montana conditions were obtained. The writer wishes to acknowledge his indebtedness to the authorities of both stations for the opportunity to study the problems, and for many courtesies extended during the work; and especially to Dr. R. N. Chapman, of the University of Minnesota, under whose direct supervision most of the Minnesota work was done, and whose advice and assistance have been invaluable. He also wishes to thank Mr. U. G. Purssell, Mr. C. M. Ling, and Mr. W. T. Lathrop, Meteorologists of the United States Weather Bureau at Minneapolis, Havre, and Helena, respectively, for their co-operation in supplying meteorological data used in these studies.

METHODS USED

In a previous paper (Cook '21), the author published the Minnesota data relative to the effects of weather upon moth flight, using the method of partial correlation in their interpretation. This paper

extends this discussion, using similar methods in this part of the work. These methods are well explained in Yule ('19) and Smith ('20). The method of correlation depends upon the basic assumption that the relation between the factors studied lies along a straight line, which is approximately the case with the moth flight data, with the same exception noted in the previous paper ('21, p. 53). Partial correlation assumes a casual relationship between the factors correlated, which is justified in the work on moth flight, but can not be readily assumed in the work on the relation of climatic conditions to larval growth, so that in this latter case, only total correlation is used. It was found, upon plotting the points of the general climatic relations shown in Plate IV, that these did not lie along a straight line, so a curve was fitted to them by the method of least squares (Leland '21). Several other somewhat simpler but less accurate methods may be found in Lipka ('21), which is a valuable aid in this sort of work.

In any study of the relation of organisms to their environment, it is necessary to develop some method of correlating laboratory experiments with field observations. The laboratory experiment shows what the organism will do in a certain controlled environment, while the field observation shows what it does under constantly fluctuating conditions. If we can reduce the field condition to some sort of an expression representing the optimum condition and can determine the optimum under controlled conditions, then we may say that the two conditions are equivalent. Because of the wide fluctuations in field conditions, it is necessary to treat the mean of a large series of observations instead of using a single observation, and the only available method of determining field relations is that of statistics, which has wide social and biometric applications. The accuracy of the result varies as the square root of the number of observations, so that long series of data yield more accurate results than short series.

COMPARATIVE CLIMATOLOGY OF MINNESOTA AND MONTANA

The studies on which this paper is based were carried on under two essentially different climatic conditions, and these differences are best brought out by a comparison. It is difficult to compare two large areas, so the two points where moth flight experiments were conducted were selected as typical, and their climatic features compared.

St. Paul, Minn., is in latitude 44° 58′ N, longitude 93° 03′ W; and Havre, Mont., in latitude 48° 34′ N, longitude 109° 40′ W. Both of these general regions are in the Transition Zone of Merriam ('98), but

are considered as separate faunae by Thompson-Seton ('09), who places Minnesota chiefly in the West Alleghenian fauna and Montana chiefly in the Campestrian fauna. Table I, the data for which were secured from Henry ('06), shows the nature of the climatic differences between the two regions, and Figure 1, Plate I, is a climograph constructed from the data of Table I.

TABLE I

CLIMATOLOGY OF HAVRE, MONT., AND ST. PAUL, MINN.

Month	Temperature				Humidity 7 p. m.		Total monthly Precipitation	
	Mean monthly		Daily range					
	Havre	St. Paul	Havre	St. Paul	Havre	St. Paul	Havre	St. Paul
	Degrees	Degrees	Degrees	Degrees	Percent	Percent	Inches	Inches
January	13	12	19	18	76	76	0.8	1.0
February	14	16	21	17	77	76	0.5	0.6
March	27	29	21	18	70	68	0.6	1.6
April	44	48	24	20	44	54	1.0	2.5
May	53	60	25	20	45	51	2.1	3.3
June	61	66	24	19	43	56	2.9	4.4
July	68	74	27	21	35	54	2.1	3.6
August	66	72	29	20	34	55	1.3	3.4
September	55	62	27	20	44	58	1.1	3.3
October	44	50	24	18	56	62	0.6	2.5
November	28	32	21	16	71	69	0.7	1.2
December	22	20	19	16	75	76	0.5	1.2
Mean annual	41	45	23	18	56	63	. . . .	. . . .
Total annual	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	14.2	28.6

GENERAL CLIMATIC DATA

Temperature	Havre	St. Paul		Havre	St. Paul
Mean maximum, degrees..	53	56	Average date		
Mean minimum, degrees..	30	36	last spring frost	May 17	May 6
Absolute maximum, degrees	108	104	first fall frost	Sept. 18	Oct. 5
Absolute minimum, degrees	−55	−41	Average length of		
No. days above 90°	20	7	growing season, days.	124	152
No. days below 32°	168	158			

The climograph is a diagram originally introduced by Ball ('10) and modified by several workers, of whom Varney ('20) is one of the latest. The mean monthly figures for temperature and humidity are plotted against each other, and the dots for the successive months are connected by a line with arrowheads showing the direction of change in the annual cycle. A recent contribution by Flanders ('22) gives many variations in the use of the climograph for planting various pairs of weather factors.

The summer humidity conditions are radically different in the two regions, the period from April to September representing in Montana a condition of dryness never reached in Minnesota. This dry summer condition practically eliminates the possibility of two-brooded species, so that few such species occur in the plains region of

Montana. Another factor of considerable importance in the ecology of the moths is the large diurnal temperature range in Montana, which restricts flight to the late afternoon and early evening during a large part of the summer season. Winter conditions are very similar in the two regions, so that this factor should not operate to differentiate the two faunae.
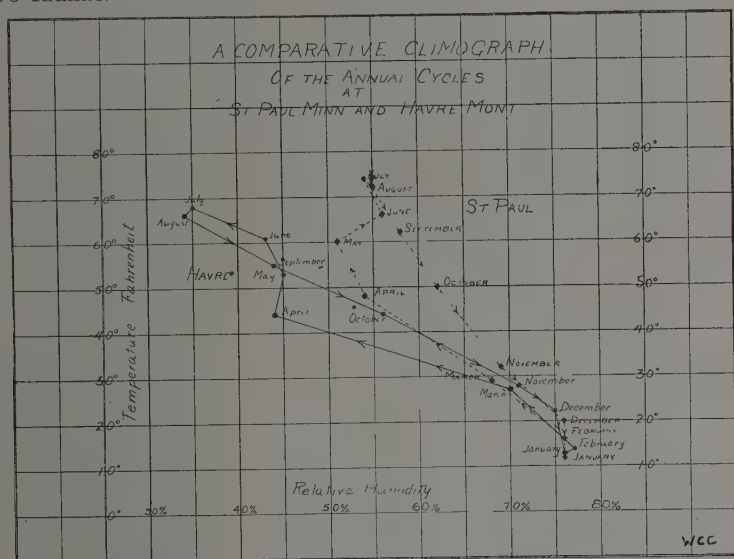
Plate I. Comparative Climatology

Figure 1. A comparative climograph of the annual cycles at St. Paul, Minn., and Havre, Mont.

GENERAL ECOLOGY OF THE NOCTUIDAE OF MINNESOTA AND MONTANA

As would be expected from the radical climatic differences, the Noctuid faunae of the two regions are essentially different, as is brought out in Table II, which is a compilation from Hampson ('03-'09). The species listed as western or eastern are not confined to Montana and Minnesota, but represent roughly semi-arid west and humid east. In order to show the relations of these regions to the generic centers of dispersal, the number of Palearctic species in each genus is included. Roughly, that region showing the greatest number of species is generally the center of dispersal (Folsom '06, p. 383).

The predominating western genera are of western origin, apparently, and none of their species is common to Europe and America, while the typical eastern genera are obviously of European origin. In this connection it is interesting to note the comment of John B.

Smith ('90, p. 11) with regard to the character of our American Agrotid fauna:

"It is suggestive that so large a proportion of our species are from the western part of our country, and that those species are mostly referable to those genera in which the front is modified in some way and the tibial armature heavy. In fact, the distinctive character of our western fauna is shown in the very predominance, and sometimes abnormal development, of tibial and clypeal armature."

TABLE II
Noctuid Distribution in the Holarctic Realm

Genus	Number of nearctic species			Number of	
	Eastern No. America	Western No. America	Common to both	Palearctic species	Holarctic species
Euxoa	25	163	10	84	0
Chorizagrotis	0	5	0	4	0
Porosagrotis	1	12	1	0	0
Feltia	7	11	1	3	0
Polia	34	63	2	71	0
Agrotis	22	17	0	79	3
Cirphis	7	7	0	66	3
Parastichtis	12	9	1	16	0
Agroperina	5	3	1	1	0
Sidemia	1	2	1	9	0
Totals					
Western group	67	254	14	161	0
Eastern group	47	38	3	171	6
Grand totals	114	292	17	332	6

The species of Euxoa, Chorizagrotis, and Porosagrotis are regarded by Hampson as representing the highest development of the Noctuid type, and this structural position is borne out by their ecology. They differ from the eastern species in many important respects, in all of which they are more highly specialized than the latter.

LARVAL HABITS

Cutworms may be grouped in three classes according to feeding habits. Climbing cutworms climb plants, eating the foliage without always destroying the main stem. *Lycophotia margaritosa* and *Porosagrotis vetusta* belong to this class. (Slingerland.) The great majority of the eastern species feed at or just above the surface of the ground, and may be called surface cutworms. Examples of this type are *Feltia ducens, Euxoa messoria,* and *E. tessellata.* A third and more recent type in point of development is the group of sub-surface feeders, or subterranean cutworms. Among the comparatively few species known to have this habit, is *Porosagrotis orthogonia* and, possibly, *Sidemia devastator. P. orthogonia* feeds entirely below the surface, cutting off plants from one to two inches below the surface of the soil, and moving from one to another underground, except under

abnormal conditions such as heavy rainfall. All the most abundant Montana cutworms are either surface or subterranean feeders, with several species suspected of the latter habit, altho this has not been proved except in the case mentioned.

ADULT HABITS

In the habits of the adults as well as in those of the larvae, the species of the two regions are quite different. In the first place, the cutworm moths of the Montana group are very strong in flight. This was well shown during the early summer of 1921, when thousands of specimens of *Chorizagrotis auxiliaris,* the Western Army cutworm, were captured in Minnesota, Iowa, and Kansas. This species breeds normally in the plains region of Montana (Cooley, '16) and has never been reported in large numbers east of that region. This means that in 1921 the moths must have flown at least three hundred miles from the place where they emerged.

Another peculiarity in the life history of *C. auxiliaris* and *Agrotis unicolor* Walk. (*Noctua clandestina* Harris), as recorded by Strickland ('16), is the habit of aestivation in the adult stage. The moths emerge in June and aestivate for a period of at least three months before maturation of the ovaries and oviposition. None of the common Minnesota species (with the possible exception of *A. unicolor,* which also breeds in Minnesota) are known to have any similar habits. This aestivation is apparently the method chosen by these species to escape the intense heat and drought of July and August in Montana.

Very little is known concerning the oviposition habits of Noctuidae, but all the eastern species whose habits are known lay their eggs directly on green vegetation. This is definitely known for *Agrotis ypsilon, Feltia ducens, Polia lorea, Lycophotia margaritosa,* and *Cirphis unipuncta.* Those Western species whose habits are known, on the other hand, lay their eggs either on trash on the surface of the soil (*C. auxiliaris,* Strickland '16), or in the surface layer of the soil. (*P. orthogonia,* Parker, Strand, and Seamans, '21). Several species of Euxoa are suspected of similar habits, but have not been found ovipositing as yet.

In reproductive capacity the Eastern species in general outrank the Western, with some exceptions. Thus, it was found in Insectary work at University Farm that *L. margaritosa* lays as many as 3000 eggs, an average figure obtained from twenty-eight moths being 1497. *Felita annexa* (Jones, '18), lays as many as 1300 eggs, an average for ten females being 794. *C. unipuncta* has been captured with as many as 800 eggs in the ovaries (Turner '18), and probably lays many more in

the field. Among the Western species, *P. orthogonia* averaged 31[
eggs each for five females (Parker, Strand, and Seamans, '21), an[
C. auxiliaris laid about 1000 eggs (Strickland '16), which figures ar[
the only ones available for Western species. It is evident that *P*
orthogonia, the most highly developed cutworm ecologically, does no[
need so high a reproductive capacity, as the eggs, being scattered i[
small clusters through the soil, have a much larger chance of surviva[

Another factor to be considered in connection with reproductive
capacity is the ability of the species to produce sudden and severe out-
breaks. A species with a high reproductive capacity can multiply very
rapidly, and a small number of moths surviving a hard winter car
quickly bring up the population to a destructive number. Such species
as *C. unipuncta* and *C. auxiliaris* and *L. margaritosa* can produce these
sudden severe outbreaks, as is evident from a superficial survey of the
general economic literature. On the other hand, *P. orthogonia* does
not suddenly appear in large numbers, but produces a gradually
increasing population in any given place until checked by climatic con-
ditions, when the cycle is recommenced.

PHYSICAL ECOLOGY OF IMMATURE STAGES

LABORATORY STUDIES

In order to obtain some experimental evidence with regard to the
relations of the various stages of Noctuids to temperature and
humidity, laboratory experiments were carried on at University Farm,
St. Paul, during the winters of 1919-20 and 1920-21. It was the inten-
tion of the writer to rear as many species as possible under controlled
conditions, but *L. margaritosa* was the only species which was obtained
in large enough numbers for this work. As atmospheric humidity has
a very small influence on the insect during the larval stages, which are
spent in the surface layer of the soil, the moisture of the direct
environment, namely, soil moisture, was studied instead.

SOIL MOISTURE RELATIONS

The method used in determining the relations of *L. margaritosa* to
soil moisture were in general those of students of plant physiology,
being the rearing of the insect in a cage of soil whose known moisture
content was held approximately constant by the daily addition of suf-
ficient water to maintain a constant weight. Lantern globes covered
over the top with coarse muslin were placed over the soil in a pot hold-
ing about five pounds of soil. The original moisture content of the
soil was determined, sufficient water added to secure the required
moisture content, the weight of pot, soil, and cage taken and held

constant throughout the experiment. The freshly-laid eggs were placed on the surface of the soil in the cage, and the insects reared to the adult stage under the same constant moisture condition. A thermograph was kept in close proximity to the cages to give a continuous record of air temperature, and all cages were kept close together in the greenhouse under as uniform conditions as possible. Two sets of experiments were performed, differing slightly in details, and will be considered separately.

First experiment—1919-20.—In this experiment three soils were used, a course sand with a maximum water capacity of about 32 per cent of dry weight; a rich leaf mold with a water capacity of about 52 per cent of dry weight; and a mixture of equal parts of these two, designated as loam, whose water capacity was about 41 per cent of dry weight. Two cages were held at each moisture condition, of which there were sixteen. The cages were examined each morning, and the number and instar of the larvae present noted, so that the figures given represent an average for the larvae of each two cages.

TABLE III

MOISTURE RELATIONS OF LYCOPHOTIA MARGARITOSA

FIRST EXPERIMENT, 1919-20

Water Content per cent of		No. of eggs	Egg period	No. of larvae	Larval period	No. of pupae	Pupal period	No. of adults	Total life	Mortality
Dry weight	Total capacity									
			days		days		days			days Per cent
				SAND	SERIES					
5.0	15	50	6.0	30	53.0*	0	....	0	59.0*	100.0
7.5	23	17	8.0	14	36.5*	1*	....	0	44.5*	100.0
10.0	32	24	7.0	13	22.3*	0	....	0	29.3*	100.0
12.5	39	18	8.0	12	59.6	2	24.5	2	89.5	96.4
15.0	47	60	7.0	52	58.1	7	22.3	3	92.3	95.0
20.0	63	27	9.0	20	52.5	4	32.0	1	91.0	96.3
Series		196	7.3	141	56.9	14	25.6	6	91.2	96.9
				LOAM SERIES						
5	14	30	7.0	2	8.0*	0	....	0	15.0*	100.0
10	28	30	7.0	14	47.1*	0	....	0	54.1*	100.0
15	42	30	6 0	23	55.6	4	23.2	4	81.2	86.7
20	56	34	7.0	19	51.9	9	23.0	8	76.2	76.2
25	70	28	9.0	14	53.8	4	32.0	2	89.0	92.9
35	98	36	9.0	6	52.7	2	22.0	1	82.0	88.9
Series		191	7.5	78	52 2	19	24.3	15	84.4	92.1
				LEAFMOLD SERIES						
10	19	27	7.0	20	56.5	1*	....	0	63.5	100.0
20	38	28	8.0	22	50.6	1	25.0	1	92.0	88.9
30	57	26	8.0	12	33.0+	0	....	0	39.0+	100.0
40	76	17	8.0	10	48.0	4	23.6	3	80.0	82.4
Series		98	7.7	54	48 3	6	23.9	4	83 0	95.9

*Insects apparently died from lack of moisture before emerging as adults.
+Larvae in this cage killed by a fungous disease.

Considering both duration of stages and mortality, the loam was the most favorable soil for growth. The minimum water requirement of the species seems to be about 35 per cent of the total capacity on each soil, and the optimum is above 50 per cent. There seems to be

no upper limit, altho probably a very wet soil is more favorable to the development of fungi in the field, thus reducing the numbers of insects.

Second experiment—1920-21.—The second set of experiments was run as a check on the first, and was conducted in the same greenhouse, under the same general conditions. Only one soil, a loam mixture with a water capacity of 32 per cent, was used, and five cages were run at each of six moisture conditions. In addition to the thermograph as in the first experiment, readings were taken each morning of the temperature of the surface soil in each cage, from which the departure of that temperature from that of the thermograph was computed and the actual temperature condition in the cage determined. Records were kept only of dates of hatching of eggs and emergence of adults, together with the number of adults emerging, from which the mortality percentage is calculated. The results of this experiment are given in Table IV.

TABLE IV

MOISTURE RELATIONS OF LYCOPHOTIA MARGARITOSA
SECOND EXPERIMENT, 1920-21

Water content Per cent of		No. of eggs	Egg period	Larval and pupal period	No. of adults	Total life	Mor-tality
Dry weight	Total capacity						
			days	days		days	Per cent
5	15	128	7	59.4	15	66.4	88.3
10	31	108	7.5	68.5	13	76.0	87.9
15	47	80	7.5	75.1	11	82.6	86.2
20	62	99	8.5	76.6	25	85.1	74.8
25	78	85	9.0	83.6	12	92.6	85.9
30	94	90	9.0	78.6	21	87.6	76.7

The minimum moisture requirement is not so evident in this experiment as in the first, but there is a definite optimum moisture of about sixty per cent of capacity. In order to show the general trend of both experiments, the data of Table III are combined with those of Table IV to form Table V, in which the various moisture contents are grouped into four general classes.

TABLE V

MOISTURE RELATIONS OF LYCOPHOTIA MARGARITOSA

Water per cent of total capacity	No. of eggs	No. of adults	Total life	Mortality
			Days	Per cent
0 to 35	314	28	71.0	93.2
36 to 50	222	21	84.8	90.5
51 to 65	183	34	85.3	81.4
66 to 100	256	39	88.5	84.8

The general conclusion to be drawn from these experiments is that the Variegated cutworm has a definite moisture requirement, both optimum and limiting, and that the optimum condition is about sixty per cent of the total water capacity of the soil.

TEMPERATURE RELATIONS

Experiments were planned for the rearing of all stages of *L. margaritosa* under controlled conditions of temperature, but it was found that any obtainable constant temperature was too high for the larval and later stages. The mortality was 100 per cent at all temperatures above 23° C., and only a single adult was secured at this temperature. Experiments on the hatching of the eggs were more successful. Table VI shows the results obtained from the exposure of twenty-four masses of 50 to 400 eggs each to three different constant temperatures. Four of the masses exposed to 30° C. failed to hatch, and only a portion of the eggs in the other six masses hatched, showing that this temperature approaches the upper limit of growth. The figures for duration of egg period are weighted according to the number of individual eggs in the experiment. The figures in the columns headed "Index of development" and "Thermal constant" are derived as explained in the introduction in the discussion of the work of Sanderson and Peairs ('13).

TABLE VI

TEMPERATURE RELATIONS OF LYCOPHOTIA MARGARITOSA

EGG STAGE

Temperature (C)		No. of masses	Duration			1/(6) Index of development	(2) x (6) Thermal constant
Observed	Effective		Max.	Min.	Mean		
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Degrees	Degrees		Days	Days	Days		
23	14.2	10	5.5	5.0	5.2	.192	73.84
27	18.2	4	4.0	4.0	4.0	.250	72.80
30	21.2	10	4.5	4.0	4.1	.244	86.92

In the second series of moisture experiments, daily readings were taken of the temperature of the surface soil of each cage, from which the actual cage temperature was computed. In Table VII are given these temperature figures for the egg stage, together with the data on duration of the egg period and computations of the index of development and thermal constant on the basis of effective temperatures, as in Table VI.

The results of both these experiments are plotted on Plate II, the points for the two series being distinguished by the use of two symbols. The agreement of the two sets is more than accidentally

close, and we must conclude that moisture in itself has little influence
on the egg stage, except as it acts indirectly, by reducing temperature.
Figure 1, Plate II, shows the temperature hyperbola drawn through all
the points, and Figure 2 shows the reciprocal line.

TABLE VII

TEMPERATURE RELATIONS OF THE EGG STAGE OF LYCOPHOTIA MARGARITOSA
UNDER CONTROLLED MOISTURE CONDITIONS

Water per cent of total capacity	No. of eggs	Egg period	Temperature (C)		Index of development	Thermal constant
			Mean, air	Mean, cage		
			Degrees	Degrees		
15	189	7.0	20	19.88	.143	77.56
31	157	7.5	20	18.99	.133	76.43
47	163	7.5	20	18.26	.133	70.95
62	156	8.5	20	17.15	.118	70.98
78	85	9.0	20	16.44	.111	68.76
94	90	9.0	20	16.52	.111	69.48

FIELD AND STATISTICAL STUDIES

Very early in the course of these studies, in considering the rela-
tions of *L. margaritosa* to temperature and soil moisture, it became
quite evident that a knowledge of these optimum and limiting condi-
tions should be of great value in a study of the relations of meteoro-
logical factors to insect outbreaks. For example, knowing definitely
that the optimum soil moisture condition for this species is about 60
per cent of the total moisture capacity of any soil, would it not be a
logical step to assume that field conditions during a destructive out-
break must at least approach this condition? If this assumption is
correct, and the writer believes it to be, then, working back from this
hypothesis, the weather data, in terms of temperature and precipita-
tion, for the infested region during the period of the outbreak, must
represent this optimum. This, then, is the first problem. Is there any
definite indication of an approximately constant moisture condition in
the field, as expressed in the temperature and precipitation records,
and, if so, in which parts of the life history of the insect is this relation
most pronounced? Further, if possible, it is desirable to analyze the
weather data for the period covered by the destructive generation of
the insect and by the preceding winter generation, that is, for a period
extending at least a year previous to the outbreak, comparing condi-
tions in all months, in order to obtain indications of any relationships
which might aid in the climatological interpretation of the outbreak.

As it is necessary to deal with a large body of data in order to
obtain trustworthy results, it is evident that some method of analysis,
preferably some well-known standard method, must be used. For this
work the method of correlation, as developed by the writers referred
to in the introduction, is well adapted. The meteorological relations of

C. unipuncta in Minnesota have been quite carefully analyzed by this method, and some of the more general relations of *L. margaritosa* and *P. orthogonia*, altho the work done on these last two species is of a preliminary nature, introduced in this paper for purposes of comparison.
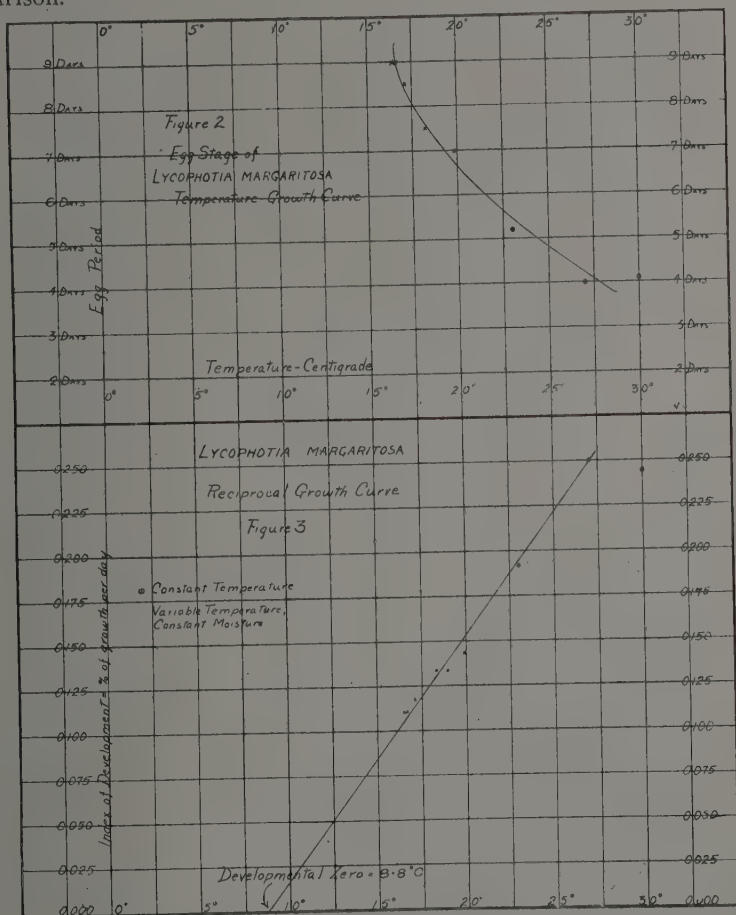
Plate II. Temperature Relations

Figure 2. Hyperbolic temperature-growth curve for the egg stage of *Lycophotia margaritosa*.

Figure 3. Reciprocal growth curve for the egg stage of *Lycophotia margaritosa*.

METEOROLOGICAL RELATIONS OF CIRPHIS UNIPUNCTA

Since 1895 there have been five major outbreaks of the army worm in Minnesota, which form the basis of this study. The general method of attack consisted in determining first the distribution of the insect in each outbreak, plotting the area roughly on a map, selecting all the United States Weather Bureau stations inside this area, and assembling the weather data for each station for the entire year preceding the outbreak. Out of about seventy-five station records so secured, twenty-one points were selected which had been in the area of destructive abundance for at least two of the five outbreaks, and their records were assembled for the entire period, 1895-1920. As some of the records were not complete for the entire year preceding an outbreak, those incomplete records were eliminated, leaving a series of thirty-five records, which were finally used as the basis of the statistical study. This elimination secured a set of records from a single region, each one represented more than once in the series, and all of them in regions more than normally liable to army worm attacks. A description of the area covered by each outbreak, the sources of information concerning each, and a list of the stations used for each in the statistical work follows.

1. 1896. A very widespread and destructive outbreak occurred throughout the southern and southeastern parts of the state. Data in regard to distribution were obtained chiefly from files of the daily newspapers of the region for the period, on file in the Library of the Minnesota Historical Society. The stations used were Farmington, Luverne, Montevideo, and Winona.

2. 1906. A more local outbreak occurred in the southwestern part of the state, extending some distance north of the Minnesota River into the southern portion of the Red River Valley. The distribution of the insect in this and succeeding outbreaks was obtained from records and correspondence filed in the office of the State Entomologist. The stations selected were Alexandria, Bird Island, Fergus Falls, and Morris.

3. 1910. A widespread outbreak occurred over the same territory covered in 1896, but with the most severe damage in the southwestern part of the state. The selected stations were Alexandria, Bird Island, Fairmont, Fergus Falls, Montevideo, Morris, New Ulm, Redwood Falls, and Windom.

4. 1919. A very widespread and severe outbreak of the army worm, accompanied almost universally by *L. margaritosa,* covered the entire southern part of the state and extended up the Red River Valley as far as Crookston. This outbreak and the one in 1920 were per-

sonally investigated by the writer. Selected stations were Albert Lea, Bird Island, Fairmont, Farmington, Grand Meadow, Luverne, Lynd, Montevideo, New Ulm, Redwood Falls, St. Peter, Winona, Worthington, and Zumbrota.

5. 1920. A locally severe outbreak occurred over an area embracing portions of the counties of Rock, Pipestone, Murray, Cottonwood, Lyon, and Redwood. The stations chosen were Bird Island, Luverne, Lynd, and Montevideo.

Complete data for these stations may be found in the files of the "Climatological Data, Minnesota Section," of the United States Weather Bureau.

Having assembled these data, the next step is the search for some methods of interpretation which will bring out the presence of a given moisture condition such as was outlined above. A consideration of the relationship between temperature, precipitation, and soil moisture makes it evident that, considering the variation in the evaporating power of the air at different temperatures, a heavy precipitation at a high temperature would produce the same moisture condition in the soil as a lighter rainfall at a lower temperature. That is, for example, the moisture at 70 degrees F. and four inches precipitation would probably be equivalent to that at 60 degrees F. and three inches rainfall. In other words, if we plot the temperature and precipitation figures for the thirty-five stations on a dot chart, whose ordinate is temperature and whose abcissa is precipitation, placing a dot at the intersection of the axes representing the condition at each station, a positive correlation between temperature and precipitation would represent the presence of an approximately constant moisture condition at all the stations. The closer the relationship, and the nearer the dots approach a straight line, the higher the value of the coefficient of correlation, "r," and the more critical this relationship in the economy of the species.

A series of dot charts, constructed as outlined above, were prepared for the conditions in each month of the year preceding an army worm outbreak, each chart containing the thirty-five points representing the selected stations. The correlation coefficient, "r" was calculated for each chart, together with its "probable error." The significance of "r" is related to its probable error, a value less than three times the probable error being of little significance, and one of more than six times the probable error indicating a very critical relationship. In order to determine whether these correlations were entirely due to the conditions in years preceding army worm outbreaks, a second series of charts was constructed, one for each month, on which the temperature

and precipitation for the twenty-one stations for the entire period of twenty-five years were plotted. The difference between the correlations in the latter set and those in the former set indicated the true relationship of these conditions to army worm outbreaks. Both sets of coefficients and probable errors are given in Table VIII. Those months in which the value of "r" was near to six times its probable error, and in which it varies greatly in the months preceding army worm outbreaks from the value for the same month in the whole period, are regarded as critical, and the month and value are repeated in the fourth column.

TABLE VIII

CORRELATIONS OF TEMPERATURE WITH PRECIPITATION

Month	21 Stations entire period 1895-1920	35 Selected stations for period preceding army worm outbreak	Significant correlation or critical period
August.............	$+.129 \pm .031$	$-.007 \pm .113$	
September..........	$+.038 \pm .033$	$+.421 \pm .093$	$+.421$ September
October............	$-.064 \pm .033$	$+.571 \pm .077$	$+.571$ October
November..........	$+.029 \pm .033$	$+.481 \pm .088$	$+.481$ November
December..........	$+.017 \pm .033$	$+.135 \pm .112$	
January............	$-.251 \pm .031$	$-.227 \pm .108$	
February..........	$+.319 \pm .030$	$+.242 \pm .107$	
March.............	$-.390 \pm .028$	$-.416 \pm .094$	
April..............	$+.012 \pm .033$	$-.318 \pm .102$	
May...............	$+.096 \pm .033$	$+.548 \pm .079$	$+.548$ May
June...............	$-.005 \pm .033$	$+.122 \pm .110$	
July...............	$-.169 \pm .032$	$+.159 \pm .110$	

Analyzing the data in this manner shows that without any reasonable doubt, there is present some definite, practically constant moisture condition during the period preceding the outbreak, and that this condition is most marked in the months of September, October, November, and May, or during the larval life of the overwintering generation. The correlations in the winter months are fairly high, but correspond closely to those for the twenty-five year series, and hence are not necessarily related to army worm outbreaks.

The next logical step would be to ascertain whether this moisture condition is approximately equivalent in the various critical months, but we will postpone this consideration until some other relationships are studied. Let us next study the relations between successive months, for the purpose of determining the presence of any seasonal succession which is of importance. A consideration of the problem will show that a negative correlation between temperature in two successive months shows the presence of a necessary constant temperature sum for those two months. That is, if a warm September is followed always by a cold October, and a cold September by a warm October, the sum of temperature for the two months will tend to remain constant, and it remains for us to determine the significance of this thermal constant in the economy of the army worm.

In order to test the presence of any such relationships, dot charts and correlations were made by combining the temperature of each month with that following, and with various other months where there seemed to be any indication of a critical relationship. The same procedure was followed with the precipitation data, and the more significant of these correlations are given in Tables IX and X.

TABLE IX

TEMPERATURE RELATIONS BETWEEN SUCCESSIVE MONTHS
PRECEDING ARMY WORM OUTBREAKS

September	October	November	December	January	June	July
September	−.924 October	−.723 +.796 November	−.665 +.781 +.557 December	−.745 +.884 +.760 +.928 January	−.619 +.785 June	−.718 +.770 +.571 +.378 +.567 +.788 July

TABLE X

PRECIPITATION RELATIONS BETWEEN SUCCESSIVE MONTHS
PRECEDING ARMY WORM OUTBREAKS

September	October	November	December	January	June	July
September	−.364 October	−.170 +.429 November		. .	−.254 +.323	−.361 +.556
			December	January	June	+.607 July

Altho no general correlations were made, as in the case of the first set of computations, it seems probable that these correlations given here are all significant, especially those between successive months. The most interesting relationships are found in the temperature conditions in the fall and early winter months. Considering first, September, October, and November, as they are the months in which the young larva prepares for hibernation, it is apparent that there is a very high correlation indicating the existence of a constant sum of temperature for those three months. If September is warm, October and November are cold, and if September is cold, October and November are warm. In order to test for the presence of this thermal constant, the mean temperature for October and November was computed and correlated with the September temperature, which gave a value of −.771 for "r." Then the mean temperature for the three months was computed for each station, and found to be 46.92, ranging from 43.6 to 49.7 F., with a standard deviation of 1.44 degrees. The standard deviations of the monthly temperatures of which this sum was composed were 3.70, 3.47, and 3.56 degrees, respectively.

The significance of this thermal constant in the economy of the insect evidently is in enabling the insect to reach a certain stage in which it is best able to hibernate. Knight ('16) has shown that this species can not hibernate in New York in the pupal stage, and evidently the range in Minnesota is even narrower, probably being restricted to two or three certain larval instars.

Another interesting temperature relationship is that between September and December and January, considered together. The relationship is even higher when October is substituted for September. This shows a very interesting balance between fall and winter conditions. If September is warm, the young larva grows quite rapidly, but its growth is checked by the cold weather in October and November, and this gradual "hardening" process enables it to withstand low temperatures in the early winter. On the other hand, if September is cold, the slow growth is accelerated during the warm October and November which follow, and the larva does not have the gradual hardening period found in the former case, and is evidently unable to withstand such cold weather in the early winter. These relationships are evidently vital to the insect, and a more complete analysis of these and others of lesser importance would probably enable us to predict the occurrence of army worms in any given locality by a study of the weather data for the previous year.

On Plate III are shown a few of these dot charts for the correlations in the fall and early winter months. The relationships are very close for this class of data, and their importance should not be underestimated. Notice particularly the high correlations between temperatures of successive periods, which are almost perfect in one case and of high value in the others.

Now, returning to the consideration of the question raised earlier in the paper as to the equivalence of the moisture conditions in the various months, we will study that point more intensively. First, it will be of value in visualizing the situation to show graphically how the condition in each of these months departs from the average of the region for twenty-five years. This is shown in Figure 4, Plate III. The heavy central axes represent the normal condition, and departures are measured from these in degrees F. and inches of rainfall. A circle represents the position of each month with regard to normal conditions. Six of the months are in the "warm, wet" quadrant, three in the "warm, dry" quadrant, and three in the "cool, dry" quadrant. None of them are in the "cool, wet" quadrant, a condition probably favorable to fungous parasites. The winter months are all warm and none of them very wet, indicating that a warm winter, with light snow-

fall, and presumably frequent freezing and thawing periods, is favorable to this species. This is also the case with the Pale Western cutworm, to be noted later.
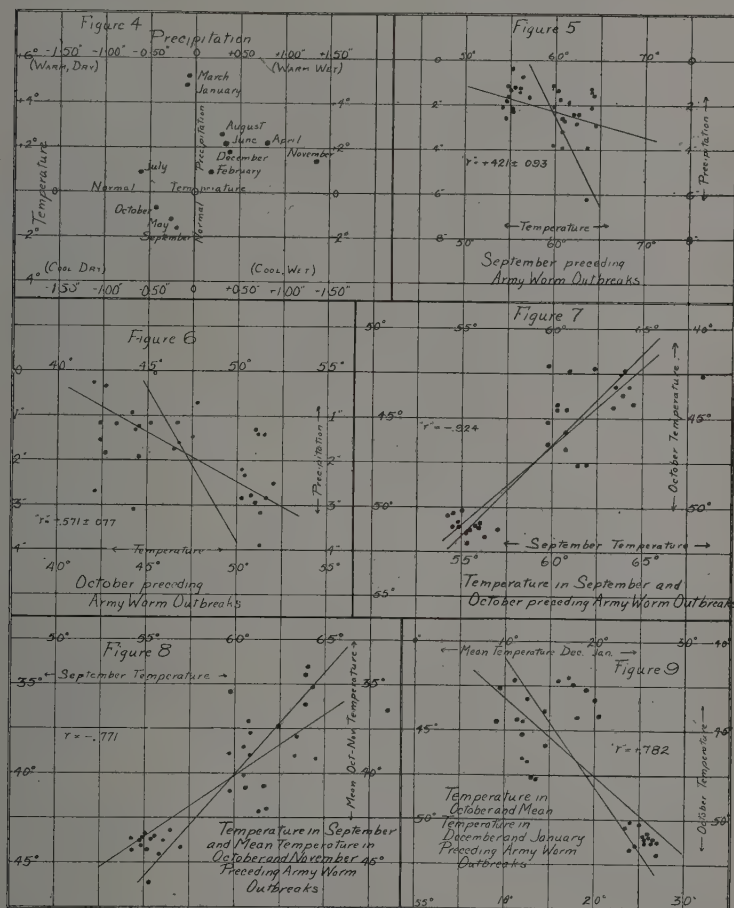
Plate III. Meteorological Relations of *Cirphis unipuncta*

Figure 4. Departures of monthly mean conditions from their respective normals during the period preceding outbreaks of *Cirphis unipuncta*.

Figures 5, 6, 7, 8, 9. Correlations between the weather factors in the period preceding army worm outbreaks.

5. September temperature and precipitation

6. October temperature and precipitation

7. September temperature and October temperature

8. September temperature and mean October-November temperature

9. October temperature and mean December-January temperature
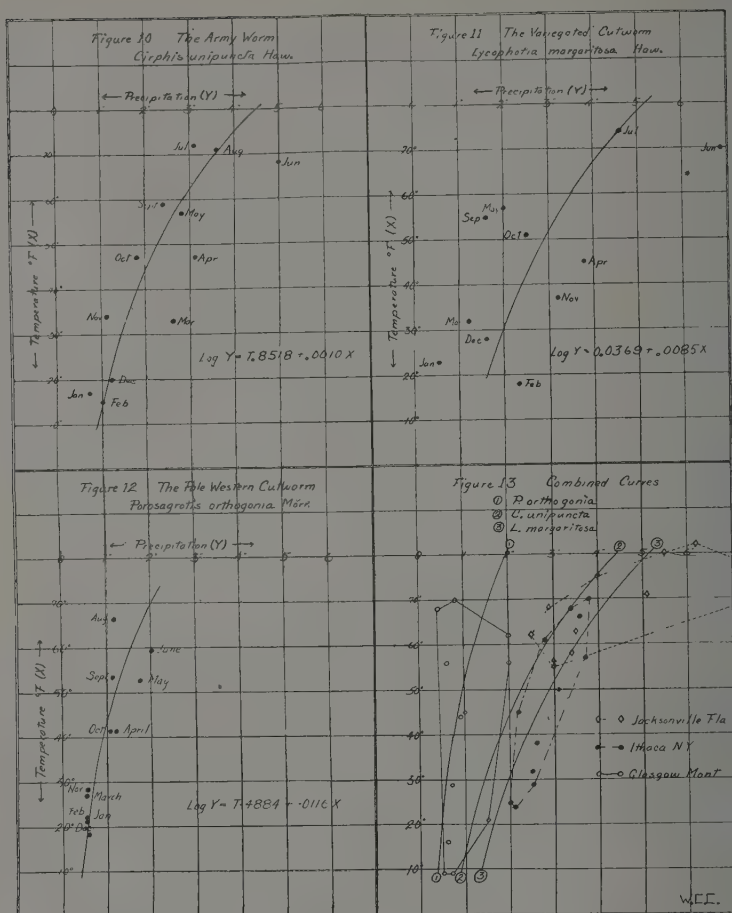
Plate IV.   Climatological Relations of Noctuidae

Figure 10.   Moisture curve of *Cirphis unipuncta*
Figure 11.   Moisture curve of *Lycophotia margaritosa*
Figure 12.   Moisture curve of *Porosagrotis orthogonia*
Figure 13.   The three curves combined, to show comparative conditions
and general distribution.

In the early part of this study, it was brought out that a positive
correlation between temperature and precipitation in any one month
indicated the existence of a nearly constant moisture condition. This
line would be approximately straight in considering the range of tem-
perature in any one month, but would probably be a curve when the
wide range of annual conditions is considered.   As the amount of

moisture in the soil is a function of the evaporation of the air as well as of temperature and precipitation, this curve should be of the same general type as the curve which shows the amount of water vapor the air can evaporate at any given temperature, in other words, the vapor pressure curve of water. The formula for this, as given by physical chemists, is approximately

$$2.3025 \; \frac{\log \; P_1}{\log \; P_0} \; = \; \frac{18.W}{1.99} \; \frac{(T_1 - T_0)}{T_0 T_1}$$

We are not primarily interested in the various constants of this curve, P representing vapor pressure; T, temperature, and W the latent heat of vaporization, but we will note that it is logarithmic in nature, and hence, if the temperature and precipitation points for the various months are plotted on a graph, they should be capable of representation by a similar logarithmic curve. Such a graph is shown in Figure 10, Plate IV, and a curve computed to fit the points, whose formula is given in the figure. The writer wishes to emphasize the point that the selection of that particular formula was the result of more or less guesswork, altho the constants are computed by least square methods, and are accurate for that type of curve. It is possible that future work will show that some other form of exponential curve will express the moisture relations of the army worm more accurately. However, the curve is semi-logarithmic, and a plot of the points on semi-log paper shows them to fall in the neighborhood of a straight line, which justifies the assumption of that type of formula.

To summarize the results of the analysis of the meteorological relations of *Cirphis unipuncta,* we may state the following conclusions:

1. The army worm evidently has a definite optimum moisture requirement, as shown by the various correlations, which can be expressed in terms of temperature and precipitation by the logarithmic formula

$$\log Y = 9.85188 - 10 + .00999 \; X$$

in which X represents temperature and Y precipitation. Substitution of given values of X in the equation give the corresponding log Y, from which Y may be found. This equation represents the general optimum condition, and any place whose annual conditions approach this curve lies within the normal range of the species, and is liable to infestation whenever the particular requirements outlined below are satisfied.

2. In Minnesota, where hibernation takes place in the larval stage, the sum of temperatures during September, October, and November must approach $3 \times 46.92°$ F.

In addition, the temperature for the two months of December and January taken together must bear the relation to that of October expressed by the equation

Dec. temp. $+$ Jan. temp. $= 3.35$ Oct. temp. $- 120.4°$

which equation is derived from the correlation in Figure 9, Plate III. The above are the most important particular requirements which must be fulfilled in Minnesota before an army worm outbreak occurs. There are probably other minor conditions which combine with these, but which are not so vital. The relation between temperature and precipitation must, at least in September, October, November, and May, approach the general condition outlined above.

METEOROLOGICAL RELATIONS OF LYCOPHOTIA MARGARITOSA

Unfortunately for this study, the only outbreak of this species in Minnesota concerning which we have definite information available was in 1919, in association with *C. unipuncta,* as was mentioned above. With only this single outbreak as a basis, it seemed futile to attempt much statistical work, as the results obtained would be of but slight value. However, a comparative study of the weather data for this outbreak and that for the other four army worm outbreaks should yield some evidence as to the points of difference which made possible the extreme abundance of *L. margaritosa.* Accordingly, the stations listed for 1919 were separated from the rest of the data, and their means computed. These figures, together with those for the Pale Western cutworm, will be found in Table XI.

These means were then plotted in a manner similar to that used with the mean figures for the army worm outbreaks, and a similar exponential curve plotted to fit them, whose equation is

Log $Y = 0.03695 + .00845$ X (Plate IV, Fig. 11)

This curve differs chiefly from the army worm curve in the size of the constant term, indicating a larger basic amount of rainfall, and showing that the Variegated cutworm prefers conditions more moist than the army worm.

Knowing from laboratory experiments that the optimum moisture condition for this species is about 60 per cent of total water capacity, we can conclude that this curve represents an approximation to this condition, and hence that the army worm curve, which represents a slightly lesser amount of precipitation for any given temperature, indicates the optimum for that species to be slightly lower, probably in the neighborhood of 45 to 50 per cent of total capacity. The writer has been unable as yet to confirm this fact experimentally, and it would be a matter of considerable interest and value to do so.

Because the data are so meager, it is impossible to draw any conclusions with regard to any necessary succession of seasonal conditions, as was done in the case of the army worm, so this part of the study is incomplete.

METEOROLOGICAL RELATIONS OF POROSAGROTIS ORTHOGONIA

The two species whose climatic relations we have been considering are both normal inhabitants of the humid region of Minnesota, and their moisture requirements are those natural to species of this region. We will now consider these relations of *Porosagrotis orthogonia,* a species whose habitat is a region with a normal rainfall of about fourteen inches per annum, as compared to twenty-eight in Minnesota. It is apparent that the moisture requirement of such a species must be very much lower than those of the former two species, but it is not at once apparent just how much lower it should be.

The Pale Western cutworm is a species which has very recently become of great importance in many parts of Montana. It was first noted in large numbers in 1915, and has since been rapidly increasing. For a sketch of its distributional history, the reader is referred to Parker, Strand, and Seamans ('21). The chief point of interest in connection with its rapid increase is the fact that the last five years (1917-21) have been a period of almost unprecedented drouth over the infested regions, which has evidently been an important factor in the ecology of the species. From distributional data on file at the Entomology Department, Montana State College, maps were constructed as in the case of the army worm, and United States Weather Bureau stations were selected as representative of conditions in the infested regions. As this study is still in the early stages, the distribution and list of stations will not be published.

Two points noted at the beginning of the study are of interest, and will be mentioned. First, a very superficial study of these distributional maps in connection with maps showing the annual distribution of precipitation for the period made it very evident that the greatest amount of damage in any year fell within the area of the state receiving less than twelve inches of rainfall. This shows beyond a doubt the semi-arid character of the optimum condition. Second, a plotting of the monthly means for a period of about a year preceding outbreaks, obtained in each case by the averaging of about forty points, gave the distribution curve shown in Figure 12, Plate IV. Computing the constants for this curve by the method of least squares gave the equation for this species as

$$\text{Log } Y = 9.48837 - 10 + .01158 \, X$$

Thus this curve, of a similar formula to the other two, varies in the size of the constant term, and also in the greater value of the X term, indicating a greater curvature than in the other cases. An inspection of this curve as plotted shows the much smaller amounts of rainfall necessary to produce the optimum for this species.

Another relation, on which very little work has been done other than a preliminary examination of the data, is the relation to winter conditions. Such an examination showed that winter conditions in years and places preceding outbreaks were warmer than normal, and drier than normal. Thus, this species, like the army worm, can withstand a considerable amount of freezing and thawing better than steady cold weather with a heavy snow blanket.

COMPARATIVE CLIMATOLOGY

Now that the general climatic relations of these three species have been outlined, it is of interest to compare these conditions with each other and with other places, to show the significance of these relations in the consideration of general distribution. Table XI gives the comparative conditions in the months preceding outbreaks of the three species studied.

TABLE XI

COMPARATIVE CLIMATOLOGY

Month preceding Outbreak	Porosagrotis orthogonia		Cirphis unipuncta		Lycophotia margaritosa	
	Temp.	Precip.	Temp.	Precip.	Temp.	Precip.
	Degrees	Inches	Degrees	Inch s	Degrees	Inches
August...........	66.5	1.2	......	......	55.3	1.6
September.......	53.7	1.1	59.4	2.2	51.0	2.5
October.........	41.4	1.1	47.0	1.8	36.9	3.2
November.......	28.6	0.6	34.1	2.6	27.7	1.6
December.......	18.7	0.6	20.1	1.1	23.2	0.5
January.........	21.1	0.5	17.6	0.7	17.5	2.3
February........	22.1	0.5	15.8	1.2	31.7	1.2
March..........	27.0	0.5	33.0	1.1	45.4	3.8
April...........	41.4	1.2	46.8	3.1	56.9	2.0
May............	52.7	1.7	56.6	2.6	56.9	2.0
June...........	59.4	2.0	68.3	5.5	69.6	6.9
July...........			72.3	3.5	74.3	4.6
Total precipitation		10.8	....	25.4	....	30.2

This table shows conclusively the wide variation in the moisture requirements of the three species, a fact which is shown graphically in Figure 13, Plate IV, on which all three of the curves are drawn in their relations to each other.

If these lines really represent the moisture requirements of these species, any location in which one of them is normally found should approach the moisture conditions indicated by the particular line. In order to test this out, three points were chosen, one of which is within range of the Pale Western cutworm, one in the range of the army

worm, and presumably, of the Variegated cutworm, and one of which
is outside of the range of the army worm, but possibly, under excep-
tional conditions in the range of the Variegated cutworm. The three
points chosen were Glasgow, Mont.; Ithaca, N. Y.; and Jacksonville,
Fla. The data for their mean monthly temperatures and precipita-
tions were obtained from Henry ('06), and plotted on Figure 13 in
their proper relation to the three curves. The lines drawn connecting
the outside points of each station are of no especial significance, but
are merely introduced to bring out the general conditions at each point
more clearly. In the cases of Glasgow and Ithaca, the points are in
very close relation to the respective cutworm curves, showing that they
normally approach the necessary moisture condition. The condition at
Ithaca is of special interest when considered in connection with the
theory of Fitch ('60) which was evolved from a study of New York
conditions. Ithaca is normally slightly to the "wet" side of the army
worm curve, which accounts for the occurrence of army worms there
following dry seasons, as Fitch has indicated.

Jacksonville is not only at a considerable distance from either of
the curves for army worm and Variegated cutworm, but the major
axis of the polygon lies at a considerable angle to these curves. Thus
it would not only take a wide variation in conditions to bring about an
army worm outbreak there, but this variation would have to be such
as would twist the axis of the distribution through a considerable
angle, a condition which practically excludes the possibility of exten-
sive outbreaks in that region.

It is hardly conceivable that either of the last two places would
ever become dry enough to be infested by the Pale Western cutworm,
or that Glasgow would ever be wet enough to be infested by the
army worm.

CONCLUSIONS

We may summarize the results of the studies on the relations of
meteorological conditions to outbreaks of these three Noctuid species
in the following statements.

1. Each of these species has a definite optimum and limiting soil
moisture requirement, which has been ascertained directly by labora-
tory experiments in the case of *Lycophotia margaritosa,* and indirectly,
by a study of conditions surrounding outbreaks in the case of the
other two species. This moisture requirement is capable of mathe-
matical expression in the form of an equation similar to that express-
ing the relation of vapor pressure of water to temperature, giving
directly the optimum condition in terms of temperature and precipita-
tion during the growth period of the species. These three equations
fitted to the data for the three species are:

A.   Pale Western cutworm....Log $Y = 9.48837 - 10 + .01158$ X
B.   Army worm..............Log $Y = 9.85188 - 10 + .00999$ X
C.   Variegated cutworm......Log $Y = 0.03695 \qquad + .00845$ X

2.   These soil moisture curves may be used to indicate the distribution of each species by plotting the mean data for any station on the same graph and comparing their location with the curve.

3.   In addition to these general moisture requirements, there are certain sequences of climatic conditions necessary for the production of the species in large numbers, which must be fulfilled in any season before an outbreak can occur. The temperature relations of *C. unipuncta* during the fall and winter months are an example of such a condition.

4.   Of these conditions, those surrounding hibernation seem to be of the greatest importance, and an outbreak seems to be directly related to the percentage of the larvae that survive the winter successfully.

METEOROLOGICAL RELATIONS OF THE ADULT MOTHS

As was already stated, the data relating to the effects of weather conditions on moth flight were secured at St. Paul, Minn., in 1920, and at Havre, Mont., in 1921. The Minnesota data were published in a former paper (Cook '21) together with a part of the present statistical treatment, and these basic data will not be repeated here.

Bait traps were run at Havre between August 1 and September 8, when a cold wave and considerable snowfall practically put an end to moth flight. The traps used were large glazed earthenware receptacles holding about five gallons each. Eleven of these were used during the height of the flight season on two fields, being placed about three hundred feet apart and about three feet above the ground. The bait used was a 10 per cent solution (by volume) of crude beet molasses, obtained from the Great Western Sugar Co., at Billings, Mont. Because of the high evaporation it was found necessary to renew the solution about twice a week.

A record was kept of the numbers caught of each of the more abundant species per night, and a comparative count of the males and females of *Porosagrotis orthogonia,* which was the species on which the most accurate data were desired. As the catches for a few nights at the height of the flight period were too large to be counted by one individual, the entire catch was preserved for each night by drying, and later counted by the following method of sampling. The entire night's catch was placed in a conical pile on a flat surface, and separated by planes through the apex into a series of radiating piles, each of which represented a definite fraction of the catch (one-fourth or one-eighth, depending on the size of the total catch). One of these piles was then carefully examined and sorted, and the rest of the catch

merely counted, the total for each species being assigned pro rata from the proportion found in the examination of the fraction. This method was found to give results of relatively high accuracy.

Table XII gives the total figures for the more abundant Noctuids, obtained as described above.

TABLE XII

Moth Flight at Havre, Mont.

August 1 to September 8, 1921

Species	No. of specimens	Per cent of total catch
Porosagrotis orthogonia.........Males	6,450	10.8
Females	14,614	24.5
Euxoa pallipennis...................	28,309	47.2
Euxoa quadridentata *...............	2,826	4.7
Sidemia devastator...................	2,537	4.3
Caradrina extima...................	681	1.1
Other species.......................	4,640	7.4
Total	60,057	100.0

*Included in this record are E. quadridentata, E. dargo, E. ridingsiana, and several other closely related species.

Included among the "other species" were *Chorizagrotis auxiliaris, Feltia ducens, Porosagrotis catenula,* and about twenty-five other species, mostly of the genus Euxoa, as well as considerable unidentifiable material. None of these species was present in more than one per cent of the total.

The noteworthy feature of the catch was the great and increasing abundance of *Euxoa pallipennis,* a species formerly very rare, but at present the most common single species. So far as is known, the species is not injurious to crops, but the larva has not been positively identified.

Records of temperature and humidity were available at the experiment station from instruments exposed to field conditions within half a mile of the traps. Pressure observations taken at 6:00 p. m. were obtained from Mr. C. M. Ling, United States Meteorologist at Havre, about seven and one-half miles distant. As pressure varies rather slowly, these readings gave a good index to conditions at the station. The data for catches, temperature, humidity, pressure, and precipitation, together with the five-day sliding average for each, computed as in the former page, are given in Table XIII. The normals, which were not computed for the weather factors in the Minnesota data as published, were also computed for these factors, but the figures are not included. Plate V is a graphical representation of Table XIII. For each factor are shown a straight line representing the seasonal mean, an angular graph showing the daily variations in the factor, and a smoother curve closely approximating the five-day normals.

TABLE XIII

Moth Flight at Havre, Mont., and Meteorological Data

| | | Moth catches | | | | 7 p.m. temperature | | | 7 p.m. humidity | | | 6 p.m. pressure | | | |
| Date | No. of traps | Total | Per trap | 5-Day normal | Per cent normal | Daily | 5-Day normal | Dept.from normal | Daily | 5-day normal | Dept.from normal | Daily | 5-day normal | Dept.from normal | Precip-itation |
(1)	(2)	(3)	(4)	(5)	(6)	(7) Degrees	(8) Degrees	(9) Degrees	(10)	(11)	(12)	(13)	(14)	(15)	(16) Inches
Aug. 1	1	44	44.0	....	....	75	....	....	42	....	....	27.421	....	....	*
2	3	38	12.6	....	....	82	....	....	30	....	....	27.271	....	....	
3	3	43	14.3	16.0	89.6	83	74	9	43	39	4	27.211	27.367	-.156	
4	4	19	4.7	8.6	54.6	64	74	-10	41	35	6	27.409	27.372	.037	
5	4	18	4.5	7.5	60.0	65	73	-8	38	34	4	27.524	27.372	.152	
6	4	29	7.2	7.1	101.3	73	74	-1	25	30	5	27.443	27.361	.082	
7	4	28	7.0	11.2	62.5	83	76	7	21	29	8	27.275	27.334	-.059	
8	4	49	12.2	20.7	58.9	84	77	7	24	29	5	27.153	27.316	-.163	
9	4	101	25.2	22.6	111.4	78	78	0	38	32	6	27.274	27.317	-.043	
10	4	208	52.0	22.1	235.4	71	75	4	39	40	1	27.433	27.381	.052	
11	4	68	17.0	20.4	83.4	75	73	2	39	43	4	27.451	27.462	-.011	
12	4	15	3.7	16.5	22.4	66	74	8	59	43	16	27.596	27.458	.138	
13	4	17	4.2	6.3	66.7	76	74	2	40	46	6	27.557	27.382	.175	
14	4	23	5.7	6.9	82.6	81	73	8	37	49	12	27.251	27.350	-.099	
15	4	5	1.2	7.9	15.2	71	74	3	54	50	4	27.053	27.257	-.204	
16	4	80	20.0	8.5	235.4	70	71	1	57	59	2	27.292	27.209	.083	0.42
17	3	26	8.6	13.0	66.1	73	68	-5	61	60	1	27.132	27.264	-.132	0.08
18	3	21	7.0	17.5	40.0	59	69	-10	84	57	27	27.316	27.313	.003	0.03
19	3	85	28.3	18.1	156.2	68	70	2	44	50	6	27.525	27.298	.227	
20	2	71	23.6	34.0	69.5	75	69	6	39	44	5	27.299	27.319	-.044	
21	4	69	23.0	49.2	46.8	74	73	-1	23	33	10	27.219	27.343	-.100	
22	7	177	88.5	60.3	146.9	70	75	5	28	29	1	27.358	27.259	-.099	
23	12	329	82.2	81.6	100.6	77	75	2	31	27	4	27.192	27.271	-.079	
24	12	590	84.3	149.1	56.5	80	76	5	26	28	2	27.226	27.299	-.073	
25	12	1,558	129.8	246.5	52.6	72	76	4	27	30	3	27.360	27.287	.073	
26	12	4,340	361.2	354.0	101.8	76	77	1	30	27	9	27.358	27.298	.060	
27	11	6,885	574.1	490.8	116.8	77	79	2	37	28	-11	27.299	27.312	-.013	
28	11	7,496	624.3	625.0	99.9	81	80	1	14	25	7	27.248	27.248	.000	
29	11	9,198	766.0	658.3	116.2	76	78	2	30	23	4	27.296	27.165	.131	0.04
30	11	8,509	794.9	594.0	134.0	83	76	4	16	20	1	27.040	27.146	-.106	
31	4	5,830	529.8	579.9	91.4	81	73	5	16	23	4	26.942	27.119	-.277	
Sept. 1	11	2,775	252.1	427.0	59.1	68	68	5	23	24	3	27.206	27.112	.094	
2	11	6,136	557.0	269.1	207.1	73	64	6	31	27	6	27.109	27.163	-.054	
3	11	9	2.2	177.5	1.2	58	63	1	35	32	3	27.265	27.247	.018	
4	11	53	4.8	174.1	2.7	60	62	3	41	35	8	27.293	27.264	.029	
5	11	778	70.7	94.5	74.9	63	60	2	32	35	22	27.360	27.282	.078	
6	11	2,606	236.8	93.9	252.1	62	55	13	35	43		27.293	27.279	.014	
7	11	1,731	157.2	92.9	169.4	68			33	55		27.200	27.285	-.085	
8	11	0	0.0	....	....	48	....	....	74	....	....	27.250	....	....	0.04
9	11	0	0.0	....	....	32	....	....	100	....	....	27.323	....	....	0.86

* Trace
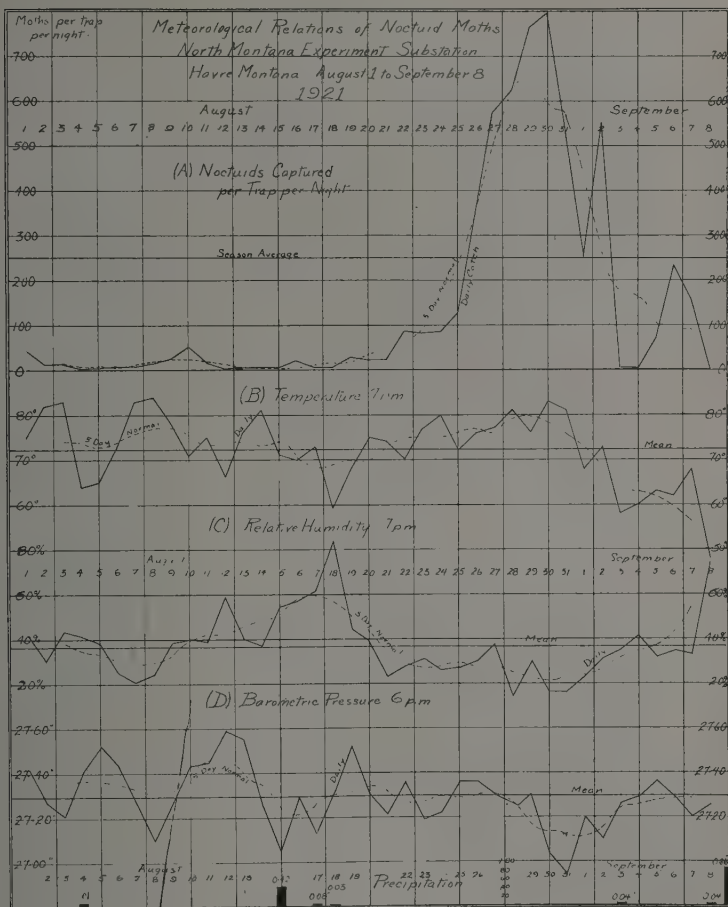
Plate V.   Meteorological Relations of Adult Moths

Figure 14.

(a)   Number of Noctuids caught per trap per night at Havre, Mont., from August 1 to September 8, 1921.

(b)   Temperature at 7 p. m.

(c)   Relative humidity at 7 p. m.

(d)   Barometric pressure at the United States Weather Bureau Station at Havre, taken at 6 p. m.

METHODS OF STATISTICAL ANALYSIS

In the first place, the object in computing the five-day normal catch was to reduce the figures for the catch from the widely varying daily figures to a common denominator, a percentage, or index number. Then similar normals were computed for the other factors for the sake of uniformity in treatment as well as for the elimination of any long-period trends. (Yule, '19, p. 200). Having these three figures for each factor, we have at our disposal three different methods of statistical treatment, which will bring out the facts from three entirely different angles. For example, a study of the relations between the index catch and the observed values of weather factors will show which particular values of those factors, if any, are most favorable to moth flight. Then, a further study of the relation between the variations in these factors and the variations in the catch will bring out any relationship between a change in any factor and the catch. Finally, a study of the relation between the departure of the normal catch from the season average and the departures of the weather factor normals from their season averages, will show the relationship, if any, which exists between the emergence of the various species and the condition of the weather during the period of emergence. All three of these methods of analysis have been applied to both sets of data, and partial correlations worked out between the catch factor and the various weather factors. These coefficients, obtained in the manner explained in the previous paper, are all given in Table XIV, on the opposite page. The coefficients are divided into three groups, indicated by the designations A, B, and C, corresponding to the three methods of analysis outlined above.

The coefficients of group A, which are the ones published for the Minnesota data in the previous paper, are intended as a measure of the relationship between the index catch and the observed values of the weather factors. It was found necessary to divide the Minnesota data on the basis of humidity, the dividing lines being below 54 per cent and above 50 per cent respectively. The same process was necessary in treating the Montana data, except that the dividing line in this case was drawn below 40 per cent and above 30 per cent. Humidity is the most significant factor in this group, and the largest index catches were secured in times when this factor was near the mean for the season. In other words, the moths flew best in times when humidity was about average for the season. None of the coefficients is large, and the Montana figures would be of little value except that they show the same tendency as the Minnesota figures.

TABLE XIV

CORRELATIONS OF MOTH FLIGHT WITH METEOROLOGICAL FACTORS

GROUP A—INDEX CATCH AND OBSERVED VALUES
(COLUMNS 6, 7, 10, 13, TABLE XIII)

Factors correlated	Humidity below optimum				Humidity above optimum			
	Minnesota (54%)		Montana (40%)		Minnesota (50%)		Montana (30%)	
	Total	Partial	Total	Partial	Total	Partial	Total	Partial
Catch-Temperature	+.34	+.28 ± .089	−.11	−.07 ± .130	+.19	+.02 ± .102	+.17	+.10 ± .140
Catch-Humidity	+.37	+.31 ± .087	+.20	+.24 ± .130	−.46	−.35 ± .089	−.27	−.24 ± .130
Catch-Pressure	−.17	−.07 ± .096	−.02	−.18 ± .130	+.18	+.09 ± .101	+.03	−.04 ± .140
Temperature-Humidity	+.25		−.45		−.47		−.25	
Temperature-Pressure	+.45		−.46		−.40		−.22	
Humidity-Pressure	−.32		+.57		−.20		+.03	
Multiple correlation	Rc. thp	+.45 ± .07	Rc. thp	+.26 ± .12	Rc. thp	+.47 ± .08	Rc. thp	+.30 ± .13

Group B—Index catch with Departures from normals
(Columns 6, 9, 12, 15, TABLE XIII)

Factors correlated	Minnesota		Montana	
	Total	Partial	Total	Partial
Catch-Temperature	+.23	+.30 ± .06	+.26	+.31 ± .10
Catch-Humidity	−.32	−.14 ± .07	−.32	−.07 ± .11
Catch-Pressure	+.18	+.24 ± .07	+.22	+.39 ± .09
Temperature-Humidity	−.13		−.66	
Temperature-Pressure	−.42		−.61	
Humidity-Pressure	−.42		+.20	
Multiple correlation	Rc. thp.	+.44 ± .05	Rc. thp.	+.44 ± .09

Group C—Normal catch with Normal climatic factors
(Columns 5, 8, 11, 14, TABLE XIII)

Factors correlated	Minnesota		Montana	
	Total	Partial	Total	Partial
Catch-Temperature	+.20	+.16 ± .07	+.30	+.02 ± .11
Catch-Humidity	+.42	+.34 ± .06	+.80	+.77 ± .04
Catch-Pressure	−.37	−.16 ± .07	−.68	−.74 ± .05
Temperature-Humidity	−.05		−.50	
Temperature-Pressure	−.35		−.03	
Humidity-Pressure	−.41		+.34	
Multiple correlation	Rc. thp.	+.48 ± .06	Rc. thp.	+.92 ± .02

Considering the coefficients of Group B, we have a much different condition. In this set of correlations, the effects of variations in the factors were studied, and variations in humidity have the smallest effect of any factor studied. Temperature and pressure both have significant positive correlations, which may be interpreted as follows: When the temperature and pressure are higher, and the humidity lower, on any particular night than the averages of these factors for the five nights of which this one is the center, then the catch is also higher than the average for these five nights. That is, moths fly more freely on warm, dry nights, following cooler, damper nights than when the reverse is true.

It is in group C that the largest values are found for the correlation coefficients. As the figures correlated are averages for five-day periods, the relations must be considered as being relations of the weather factors to emergence. Thus, under Minnesota conditions, more moths emerge in a time of higher temperature and lower pressure and higher humidity than the season average, the humidity being the most important factor, followed by temperature and pressure. In the Montana data temperature was of practically no significance, but there was a very high relationship between emergence and the other two factors, with humidity slightly more important. Evidently, more moths emerge in times of high humidity in humid regions, and more moths emerge in times of low humidity in arid regions. The size of the coefficient of multiple correlation in the latter case, "R"$=+.92$, indicates that the emergence of moths in the arid regions is almost entirely a function of these climatic conditions.

To summarize these relations; the observed values of humidity have an important bearing on the flight of moths, the largest numbers flying when the humidity is near the seasonal mean. Humidity also affects emergence, more emerging under high humidity conditions in Minnesota and under low humidity conditions in Montana. Variations in temperature and pressure from night to night are of more importance than variations in humidity. Further studies, and the accumulation of more data may affect these relationships, but probably will only intensify them.

CONCLUSIONS

A general consideration of the studies presented in this paper leads to the following conclusions:

1. Each of the species included in this study has a very definite optimum soil moisture requirement, which, broadly speaking, limits the distribution of the species.

2. This requirement may be determined experimentally under controlled conditions, and also indirectly, by a statistical analysis of the weather conditions surrounding outbreaks of that species.

3. In each case, the optimum moisture requirement of the species which occur in any given region is a close approach to the normal climatic condition in that region, so that outbreaks would occur every season were it not that there is also a necessary seasonal sequence of conditions which must be fulfilled in order to enable the insect to reach destructive abundance.

4. This sequence, which may operate either by favoring the destructive insect, by limiting the activities of its enemies, or both, is the controlling factor in the production of outbreaks, and a careful study of such a sequence in the life history of any insect should enable us to predict the possibility of an outbreak of that insect in any given region.

In conclusion, the writer wishes to emphasize the importance of the use of mathematical methods in the study of insect outbreaks, as well as to show its practical application in the examples cited. As the literature of statistics is rather foreign to entomological workers, a few selected titles of especially valuable works, which are of great service in such a study, are listed in the bibliography.

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CONTENTS

THE NORMAL AND PATHOLOGICAL HISTOLOGY OF THE VENTRICULUS OF THE HONEY-BEE, WITH SPECIAL REFERENCE TO INFECTION WITH *NOSEMA APIS*

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In the great amount of work which has been done on the organisms of insect-borne diseases and on micro-organisms found as parasites in insect tissues, the pathological histology of the insect itself has been singularly neglected. Furthermore it is found that the basis for such study—namely, a knowledge of the normal histology and cytology—is often almost entirely lacking. The fact that many of the intracellular symbionts of insects and the granule-like Rickettsia organisms of typhus and trench fever, were for some time after their discovery confused with normal cell inclusions, well illustrates the need for study of the normal histology and particularly of the granular cell inclusions universally present in insect tissues. While the primary purpose of this paper is a consideration of the pathology of the adult honey-bee, there has necessarily been included as a basis therefor, a somewhat extended discussion of the normal histology and cytology. This broader phase of the problem it is believed will appeal to the parasitologist or other worker with micro-organisms, quite as strongly as the pathology itself.

THE DISEASES OF ADULT HONEY-BEES

The diseases of bees best known to the beekeeper, and those ordinarily referred to under the term "bee diseases," especially in America, are the diseases of the larvae or brood. Of these the most common and the most serious are the bacterial diseases, American foulbrood and European foulbrood. In addition to the larval diseases, there are a great number of disorders of the adult honey-bee, accounts of which are found in beekeeping literature as far back as three hundred years. (Bullamore 1922; Zander 1911, 1921.) These disorders, nearly all of obscure etiology, are characterized by a variety of symptoms and are known to the beekeeper under a wide variety of names. Besides those conditions supposedly due to old age, exposure, insufficient or improper food, or poisoning, may be mentioned dysentery, diarrhoea, Ruhr, May-sickness, May-pest, June-sickness, paralysis, palsy, trembling, dizziness,

vertigo, spring dwindling, disappearing disease, dropsy, Sandläuferei, Fussgängerei, Isle of Wight disease, Nosema-disease, Aspergillusmy- cosis and "paratyphoid." The variety of symptoms exhibited in these disorders is indicated to some extent by their names. A review of the literature reveals the very greatest confusion as to nomenclature, the symptoms associated with a given disease, and etiology. Despite the multiplicity of names and the variety of symptoms, these disorders are all marked by one outstanding feature—namely: the affected bees, unable to fly, are found crawling or nearly motionless, usually near the hive, where they die after a few hours.

While these disorders may occur at any time of the year, they are most common in late winter and early spring, being known fre- quently as winter losses, spring dwindling, May-sickness, etc. They appear to be highly contagious in some cases and in others not at all so. There is no constant correlation of any of the disorders with such external factors as periods of unfavorable weather or the blossom- ing of certain nectar- or pollen-producing plants.

It is probable that many of the disorders which have been considered distinct pathological entities are in reality only symptoms of diseases which may be evidenced externally by a number of different condi- tions. This is well illustrated in the literature of Isle of Wight disease and of Nosema-disease, the best known of the diseases of adult bees, in which the external symptoms of nearly all the various disorders have been described at one time or another as characteristic of each of these two diseases. Indeed it would appear that the various symptoms are not specific for any disease but are evident whenever the bees are weak- ened from any cause. The causes of such weakening are not known except in the few cases where definite organisms have been described. The stricken bees may exhibit marked abdominal distention with copious defecation on combs, hive or ground, this condition being known as dysentery or Ruhr. In "dry dysentery" or "constipation," there may be abdominal distention with apparently no defecation. The feces may be thin and watery, or thick and ropy, light or dark in color and acrid or otherwise in odor. The bees appear weakened, and are found mostly on the alighting board or on the ground in front of the hive, singly or in groups, clinging to spears of grass, lying nearly motionless on the ground, or crawling about either actively or sluggishly. The bees are unable to fly, though they may leave the ground for a flight of a few inches, their progress being then a combination of active crawling and "hopping." At times certain of the legs seem to be paralyzed and are dragged along in crawling. The wings are often "dislocated," i. e., the hind wings are not hooked to the fore wings, and are capable of only an irregular trembling motion, or at best a feeble, jerky fanning.

In crawling, the bee may hold itself as if bent to one side, and may describe small circles. The terms paralysis, trembling, palsy, vertigo, etc., are used to designate these various conditions.

Nosema-disease (Nosemaseuche) is the term proposed by Zander (1911) to designate an infectious form of Ruhr (dysentery) and Maikrankheit (May-sickness), with both of which he found associated the Microsporidian, *Nosema apis,* described by him in 1909. Zander considered copious defecation the surest sign of Nosema-disease, though this symptom was frequently absent. The sudden appearance of groups of bees dying inside or outside the hive was held to be an important characteristic. White (1919) studied Nosema-disease in America and concluded that it is an infectious, though not particularly malignant disorder of the adult bees. The parasite is cosmopolitan in its distribution. In heavy infections the colonies become weak and may be destroyed. The behavior of the infected colony is similar to that of a healthy one. The individual infected bees manifest no external symptoms until actually dying, when they become unable to fly and crawl about as described above. Diagnosis of the disease is confirmed by finding the spores of the parasite in the ventriculus.

Isle of Wight disease, named from the epidemic which was first reported from the Isle of Wight in 1906, has caused great losses in the British Isles. The disease was first described as "paralysis" and "dysentery" from the symptoms most commonly observed. However, it was soon shown that these symptoms were not invariably present. Indeed the only constant symptoms were the inability of the stricken bees to fly and their ultimate death. Fantham and Porter (1912a, 1912b) in their studies on Isle of Wight disease found *Nosema apis* in more or less constant association with the disease, and together with other British workers, considered this organism to be the cause of Isle of Wight disease (Graham-Smith, Fantham et al., 1912). Rennie and Harvey (1919a, 1919b), however, while holding Isle of Wight disease to be infectious, concluded that *Nosema apis* was not causally related thereto. This has apparently been confirmed by the work of Rennie, White and Harvey (1921) who found the thoracic tracheae of diseased bees containing numbers of the mite *Tarsonemus woodi,* which they considered the cause of Isle of Wight disease. These workers have also discussed the relation of the mite to the pathology of the disease.

A number of other presumably infectious disorders of adult bees associated with micro-organisms, or otherwise, may be mentioned. In Brazilian bee-pest the bees die in great numbers as in Isle of Wight disease and Nosema-disease. While the disease has been attributed to poisonous nectar, the cause remains unknown (Zander 1911). Maassen (1916a) mentioned Aspergillusmycosis, a disease affecting both larvae and adults, caused by a species of Aspergillus. Zander (1911, 1921)

and Maassen (1919) both mentioned the larvae of a Meloid beetle, *Meloë variegatus,* as at times causing losses of adult bees. The meloid larvae are found attached to the intersegmental membranes of the abdomen, having been picked up by the bees in foraging. Maassen (1919) also reported the finding of an ameba-like organism in the Malpighian tubes of adult bees, which in one case at least was associated with the death of many bees. Bahr (1919) found a bacillus of the paratyphoid group in the intestine of adult bees which were unable to fly and which were dying in numbers. Feeding pure cultures of this organism reproduced the disease. Nosema was not found in connection with this disorder.

In America and Australia serious losses of adult bees have occurred for which no satisfactory cause could be assigned, the symptoms being similar to those described for Isle of Wight disease and Nosema-disease. *Nosema apis* is known to occur in these countries and may be partly responsible for this damage, though the presence of Nosema has not been demonstrated in all cases.

It is thus seen that there are a number of disorders in which the adult bees die in numbers, exhibiting a variety of symptoms. In some cases organisms are known to be associated with, and are perhaps the cause of, the disease. In others the cause can not be designated with certainty. None of these disorders is characterized by any outward symptom definitely diagnostic for that disease. In all cases the stricken bees are unable to fly and die in numbers. It is possible, as suggested by several investigators, that inability of the bees to fly and various other conditions accompanying their death and cited as symptoms of different diseases, may represent merely the final stage in the weakening of the bees due to whatever cause.

It would accordingly be possible to have any number of disorders of adult bees, or rather disorders due to any number of different causes, in which the outward symptoms would be the same. The evidence already cited seems to indicate that such is the case. Since external symptoms are nearly valueless in indicating the real nature and causes of diseases of adult bees, the study of internal pathological conditions would seem to promise the best basis for accurate diagnosis. This method has been pursued in certain bee diseases with which an organism is definitely associated, as in Nosema-disease. The emphasis, however, has been placed on determining the presence or absence of the parasite rather than on the condition produced in the host tissues. Even here the possibility of factors other than the parasite contributing to the pathological condition is not precluded. The fact that many stricken bees contain but a few parasites, while other apparently healthy bees are heavily infected, indicates that other factors do operate in Nosema-disease. If analysis of factors other than the known or suspected

organism is necessary in disorders where such an organism has actually been demonstrated, the need for such study is all the more imperative in those disorders of adult bees of which the cause is wholly unknown or in those which have been attributed to such indefinite factors as long winter confinement, bad weather, and poisonous pollen or nectar. A comparative study of the histology and cytology of both healthy and diseased bees would seem to be one of the most promising methods of attacking the problem.

No group of animals furnishes examples of parasitism greater in point of number and diversity of nature than the insects and other arthropods. Nevertheless most of our knowledge of these parasites concerns only the organism itself, singularly little being known of the effect of the parasite on the host. In many cases in which a parasite causes a disease of economic importance the disease itself is well understood as concerns symptoms, the causal organism, the manner of transmission, and the methods of control, while little attention has been given to the pathological histology of the host. Beyond certain of the grosser and more obvious features, the changes brought about by the parasite in the host cells and tissues and the disturbances of their functions are almost unknown.

This lack of knowledge of pathological histology is especially marked in connection with diseases of the adult honey-bee, in which the diseased conditions themselves are not well understood. As a preliminary investigation of the pathology of the honey-bee from the histological point of view the present study was undertaken with the purpose of determining what changes are brought about in the tissues and cells of the ventriculus by the presence of *Nosema apis*, and further of determining what pathological conditions this organ may exhibit in certain disorders not associated with the presence of *Nosema apis*.

MATERIALS AND METHODS

Material was obtained chiefly from the University apiary, University Farm, St. Paul, during the years 1916-17 and 1919-21, and from Cornell University apiary at Ithaca, 1917-18. Bees were taken mostly from the hive entrance, though occasionally from within the hive or from blossoms. The bees were dissected as soon after their capture as possible, usually within an hour or two. After the head was cut off, the entire digestive tract was withdrawn by seizing the tip of the abdomen with forceps and pulling gently. The ventriculus was separated from the hind-intestine and dropped into 0.75 per cent. sodium chloride solution or into Locke's solution. Another method of obtaining the ventriculus was to cut off the entire abdomen and drop it into physiological saline solution. With fine forceps sufficient of the

chitinous covering was torn away to enable the ventriculus to be removed easily. Live bees were used in all cases in order to avoid any possible effects of chloroform or other killing agent.

In examining the ventriculus in the fresh condition, the whole or a small portion of the organ was crushed beneath a cover-glass. The best results were obtained by using small portions prepared as follows: A small section, about one-half a millimeter in thickness, was removed by means of scissors, this section appearing as a small white ring (the ventriculus wall) with a brownish gelatinous mass (the peritrophic membranes) within. This brownish mass was removed entire with forceps, leaving the wall intact; or the wall itself was cut with scissors, whereupon it would turn inside out, separating itself almost entirely from the peritrophic membranes. In this manner a portion of the wall of the ventriculus could be mounted free from its contents. Hanging drops were also made by touching the cut end of the ventriculus to a cover-glass and inverting this over a hollow-ground slide. The latter method allowed prolonged examination without changes in location or appearance of the material due to drying.

Cover-glass preparations were made usually as shallow hanging drops which were observed in the fresh condition and then fixed by being dropped flat upon the surface of sublimate-alcohol, or placed over a Van Tieghem cell containing 2 per cent. osmic acid solution, and then hardened by dropping upon 70 per cent. alcohol. By the latter method the preparation could be watched during fixation. Thus by noting its location a given cell could be studied in the fresh condition, during fixation and after staining.

Sections 3 to 5μ thick were made from material fixed in sublimate-alcohol, Bouin's fluid, Zenker's fluid, Gilson's mercuro-nitric solution, Hollande's (1912) bichromate-formol solution and in osmic acid vapor. The stains used for sections were mostly Heidenhain's iron-hematoxylin, counterstained with eosin, Delafield's hematoxylin, and Romanowsky stain.* For cover-glass preparations the most successful stains were Giemsa (Gruebler's Giemsalösung) and Romanowsky.* The preparations were left in the stain from 15 minutes to 24 hours, washed in distilled water, dehydrated rapidly in 95 per cent. alcohol or in acetone, passed through xylol and mounted in balsam or cedar oil.

THE NORMAL VENTRICULUS

Determination of the changes produced in the ventriculus by the presence of parasites, or the histological diagnosis of any other pathological condition, must be preceded by consideration of the normal •

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* "Romanowsky" stain, obtained from Noyes Brothers & Cutler, St. Paul, prior to 1915: equal portions of two stock solutions, "eosin" solution and "methylene blue" solution, diluted 1 to 10 in distilled water.

ventriculus, or rather the range of different conditions exhibited by this organ taken from apparently healthy bees. The criterion by which a bee is to be judged "healthy" or otherwise, is necessarily indefinite, since bees heavily infected with parasites may be outwardly indistinguishable from uninfected bees, while other bees may die in numbers from no apparent cause. Until more exact information is available concerning disorders of adult bees, "healthy" bees may be considered those in which neither external nor internal pathological conditions are apparent and which are obtained from a strong, vigorous colony, or at least one not suffering any marked loss of bees.

The ventriculus, or mid-intestine, lies in the anterior and dorsal portion of the abdomen. It is a more or less U-shaped tube, of uniform diameter, with numerous annular constrictions. It is ordinarily yellowish or whitish translucent in appearance, with reddish brown contents which give the whole a reddish brown color, though this varies somewhat from pale yellowish brown to dark brown. A deep constriction, the proventriculus, separates the ventriculus at its anterior end from the crop or honey-sac. About the ventriculus is the tangled mass of whitish or yellowish Malpighian tubes which empty into the digestive tract at the junction of the ventriculus and the small intestine, the latter being a coiled tube of about one-third the diameter of the ventriculus.

The structure of the ventriculus has been described by a number of workers (Frenzel 1886, Snodgrass 1910, White 1919, Pavlovsky and Zarin 1922). The wall of the ventriculus is made up of a number of structures. Forming a network on the outer or coelomic surface are three layers of muscle fibers, the outer and inner layers being longitudinal and the middle layer transverse. Within the muscle layers is the basement membrane which is continuous anteriorly with that of the fore-intestine (esophageal valve) and posteriorly with that of the Malpighian tubes and small intestine. Attached to the basement membrane are the cells composing the epithelium. The epithelial cells possess many fine, more or less parallel hairs arising from their surface and extending into the lumen of the ventriculus, these constituting the striated border. In the lumen and extending the entire length of the ventriculus are the peritrophic membranes, concentrically arranged. The outer, and hence most recently formed, peritrophic membrane either lies free in the lumen, sharply differentiated from the epithelium, or merges gradually with the substance of the striated border.

The inner surface of the epithelium is not regular, but appears in section to be studded with projections or villi, between which are pits or crypts (Fig. 1). The projections are joined to each other forming a honey-comb of walls surrounding the cylindrical crypts. At the bottom of the crypts are the nidi composed of the many small regen-

ration cells, while the walls are composed of columnar or elongate-
yriform cells. Each of the latter is attached to the basement membrane
y a narrow stalk, while the free end tends to be as nearly spherical
s the surrounding cells permit. The total thickness of the epithelium
verages approximately 70μ, with extremes of 30 and 110μ. At the
ottom of the crypts the epithelium measures about 25μ in thickness.

The striated border forms a layer lining the inner surface of the
pithelium and more or less completely filling the crypts. That this
ayer is made up for the most part of many fine hairs, is seen in sec-
ons of material fixed in various solutions. In addition the hairs may
e demonstrated in almost every fresh mount and are striking in
ppearance. They radiate from one side or at times apparently from
ie entire periphery of the isolated cells (Figs. 10, 18-21).

Lying over the striated border and uniting the free ends of the
airs extends a membrane of varying thickness and somewhat indefinite
utline, staining like the substance of the striated border, though more
itensely, as if it were a condensation of that substance (Figs. 1, 3, 6
nd 8). This membrane is apparently the peritrophic membrane in
rocess of formation, since it may frequently be demonstrated to be
ontinuous with a well defined peritrophic membrane which has become
etached from the epithelium in another portion of the ventriculus.
Vhile a number of workers have considered the peritrophic membranes
o be the product of certain cells at the anterior end of the mid-
itestine (see discussion in Deegener, 1913), it would appear from the
riter's observations which in general agree with those of Pavlovsky
nd Zarin (1922) that the peritrophic membranes of the honey-bee are
ormed from the substance of the striated border, together with the
emains of cells which are given off from the epithelium in the process
f digestion, and that this formation takes place not directly at the
irface of the cells but at the free ends of the hairs forming the
riated border. Snodgrass (1910) does not mention the hairs, but
gures an "intima" with a "gelatinous mass" between the intima and
ie epithelium, the gelatinous mass apparently representing the striated
order. The "intima" or "cuticle" (Pavlovsky and Zarin) together
ith the striated border separate from the epithelial cells, shrivel and
irink and finally become peritrophic membranes. The process is
peated in the formation of each successive membrane. These lie
ie within another, appearing in section as thin, much wrinkled bands,
omewhat refractive, sharply defined in some regions, in others merging
ith a finely granular substance containing here and there remains of
oithelial cells. The peritrophic membranes stain slightly or not at all,
eing usually yellowish in color, while the granular masses associated
ith them stain with eosin. In the fresh condition the peritrophic
iembranes are seen as a reddish brown, gelatinous mass, which on

traction with forceps separates easily from the epithelium. The inner-most membrane forms a tube for the passage of pollen grains and other food, and at times portions of it pass down with the food and are found in the hind-intestine surrounding little pellets of pollen.

A long tubular fold of the fore-intestine projects into the lumen of the ventriculus, forming the esophageal valve. The basement membrane bears a layer of epithelial cells somewhat smaller than those of the ventriculus. Many of these cells are stalked like those of the ventriculus, and appear to be given off from the epithelial layer from time to time. While there is no sharp dividing line between esophageal valve and ventriculus, the cytoplasm of the ventriculus cells is markedly more deeply stained than that of the valve cells.

The contents of the ventriculus during the field season usually consist only of the peritrophic membranes and the gelatinous substance associated with them. A few pollen grains are found at times, though these apparently pass rapidly to the hind-intestine where they may be found in great numbers in all stages of digestion. When the bees are in winter quarters, or at times when cleansing flights are infrequent, the ventriculus may contain a considerable accumulation of pollen, particularly at the posterior end, together with feathered bee hairs and many micro-organisms, chiefly bacteria and yeasts. The solid portions of the contents are usually enclosed by the inner peritrophic membrane, there being no direct contact with the epithelium. Occasionally, however, there may be found in sections small groups of bacteria lying next the epithelium. Whether or not bacteria can make their way through several uninjured peritrophic membranes is not known.

The intestinal flora of the honey-bee includes a number of different bacteria and yeasts, some of which are almost constantly present (White 1906). The greater number of these organisms are found in the hind-intestine, particularly the rectum, relatively few both as to numbers and variety being found at any time in the ventriculus, except at those times when an accumulation of food material occurs as noted above. The great difference in bacterial content between mid- and hind-intestine is noticeable at once in fresh preparations, and is confirmed by broth and agar cultures. The writer has at times obtained no growth in media inoculated with a small section of wall and contents of the ventriculus, while very frequently no growth resulted in tubes inoculated with a small section of the ventriculus wall freed from the peritrophic membranes. The explanation for the slight bacterial content of the ventriculus lies perhaps in the fact that solid particles pass rapidly to the hind-intestine, and further that the contents of the ventriculus are at times rather acid, which may inhibit multiplication of organisms.

One of the most striking features encountered in examining the epithelium of the ventriculus is the extreme variation of the cells and

their nuclei as to size, shape and arrangement, and as to the character, size and number of the cytoplasmic inclusions. These variations are due not only to differences in location in the epithelium and to differences in age, as are found for example in the regeneration cells and the cells of the crypt walls, but probably also to differences in function in the process of digestion, not as yet well understood. It is correspondingly difficult, therefore, to determine just what cells are to be considered "normal" and those which may exhibit some pathological condition.

In the bee, as in most insects, cells or portions of cells are given off into the lumen of the ventriculus, these being known as secretion cells (Frenzel 1886) or sphaerocytes (Deegener 1913). These apparently contain digestive enzymes, which are liberated in the lumen of the ventriculus by the disintegration of the cells. Pavlovsky and Zarin (1922) have discussed the ferments of the digestive tract of the bee. The proliferation of the secretion cells takes place chiefly from the walls of the crypts and rarely from the nidi at the bottom. Snodgrass (1910) stated that these "discharged cellules" all contain nuclei, and believed their proliferation to be due to an active division of cells forming the walls and lips of the crypts. According to the writer's observations the secretion cells may arise in several ways:

1. In some cases it appears that the entire cell, the basal portion of which usually consists of a slender stalk, elongates greatly and finally separates completely from the basement membrane. Such a secretion cell at first differs from cells of the epithelium only in that it has become nearly spherical. This condition is seen occasionally in sections in regions where the epithelium is greatly thickened as a result of the elongation of the cells. That the individual cells are easily detached from the basement membrane is shown by the great number of large, spherical, nucleate cells, apparently uninjured, to be found in every fresh preparation (Fig. 10).

2. In both sections and fresh mounts, especially the latter, are always to be observed many spherical secretion cells without nuclei, which average somewhat smaller than the nucleate cells just described (Figs. 11-20). These may arise in several ways: A division of the cell body without nuclear division may take place, though this has not been observed. In fresh mounts there have been noted frequently, however, two or more cells, equal or unequal in size, joined together as shown in Figures 17 and 18. What is apparently the same condition has been observed in sections of the normal ventriculus undergoing great proliferation of secretion cells. Many elongate secretion cells bear on their distal extremities another secretion cell. Not uncommonly there are several cross-walls in the latter, indicating perhaps as many different stages in their formation. Whether a

division of the parent cell takes place or whether one cell is formed on the surface of the other by a process resulting in what may be compared to a blister, cannot be stated. The latter method seems probable from the fact that very frequently the "blister" is clear and homogeneous while the parent cell may contain a nucleus together with the characteristic granules described below. Both may contain such granules, however. That actual division of the parent cell does not take place is further shown in sections of the ventriculus infected with Nosema, in which the same or a similar process may at times be noted. Figure 7 shows several of the greatly elongate epithelial cells bearing on their free ends tiny cap-like cells, several of the latter containing cross-walls similar to those observed in uninfected specimens. From the fact that these tiny secretion cells contain no spores and that their cytoplasm stains much more intensely than that of the infected parent cells, it is evident that no division of the parent cell body has taken place, but rather that the cap-like cells have obtained the material of which they are composed through osmosis.

3. In nearly all fresh preparations occur isolated cells beraing a stalk. These vary in size from tiny cells a few micra in diameter to those as large as the average epithelial cell. They are without nuclei, their cytoplasm may contain the refractive granules characteristic of the epithelial cells, and the hairs of the striated border are usually, though not always, present (Figs. 19, 20). Occasionally a tiny cell of this sort is seen attached by its stalk to a larger cell which may also be stalked. As many as three or four tiny cells may be joined by their stalks, forming a chain. These recall the sphaerocytes described and figured by Deegener (1913) from the mid-intestine of the larva of *Deilephila euphorbiae*. In the honey-bee they seem to arise through a constricting off of the surface portion of the epithelial cells. The number of these stalked secretion cells varies greatly in different specimens; in some they are rare or absent while in others certain parts of the ventriculus are lined with them. The rôle which these various types of secretion cells play in the digestive processes, and the conditions which give rise to one type or another, are not understood.

The nuclei vary greatly in appearance, both in the fresh and stained condition. They are spherical, oval or rarely elongate. The nuclei of the nidi as seen singly or in groups in fresh preparations are spherical and resemble fused masses of small, more or less spherical, non-refractive granules. Frequently there are also to be observed in the nucleus one to several small masses, very slightly refractive, either spheroid or irregular in shape. The nuclei of the nidi stain more intensely on the whole than do those of the surrounding cells, and appear either as a mass of small spheroid granules, intensely stained,

or as a lightly stained granular area containing one to several large, deeply stained granules or masses with definite outlines. These latter apparently correspond to the slightly refractive masses seen in the fresh condition. Though more or less active division of these cells undoubtedly takes place, nuclei in division are rarely seen, either in fresh or stained material. Two nuclei are to be observed in cells occasionally, however. Figure 2 represents a regeneration cell nucleus with division, apparently by amitosis, nearly complete.

The nuclei of the cells forming the crypt walls when freshly dissected usually appear as spheres of a clear liquid in which are suspended a number of slightly refractive masses, spheroid or somewhat elongate. These masses may be few and comparatively large or small and very numerous. The clear body of the nucleus, which at times is not homogeneous but is indistinctly granular, may or may not be liquid. However, the suspended masses appear to be firmly held, since they never exhibit Brownian movement as do the granules in the cytoplasm. The nucleus seems to be less easily destroyed by mechanical means than the rest of the cell, since many isolated nuclei, quite intact, are to be found in fresh mounts. The appearance of the nucleus fixed in osmic acid vapor is generally little changed from that of the fresh nucleus, the body of the nucleus being homogeneous or finely granular, and staining lightly, while the suspended masses stain deeply (Fig. 3). Nuclei fixed by methods other than osmic vapor in general appear either coarsely granular or coarsely reticulate (Fig. 1). Lewis and Lewis (1915) obtained similar results in fixing chick embryo cells, finding that only with osmic acid vapor was the appearance of the fresh nucleus faithfully preserved, while other fixers yielded the reticulate "text-book" nucleus.

Another condition of the nucleus is often to be observed in any one of the different types of epithelial cells, in both fresh and stained preparations. The nucleus is spherical or oval and contains what appears to be a clear homogeneous liquid. Suspended in this liquid or lying at one side of the nucleus, is a dense, granular, spheroid or irregular mass, the granules being slightly refractive with indistinct outlines (Figs. 10, 22, 23, 25). When stained such nuclei appear as vacuoles containing a densely stained, granular body.

THE CYTOPLASM AND ITS INCLUSIONS

The cytoplasm itself, whether of the nucleate epithelial cells or of the discharged secretion cells, is generally a clear, colorless liquid, though at times it is indistinctly finely granular. Its liquid or semi-liquid condition together with the very thin, elastic cell membrane, allows the cell to assume almost any shape in response to pressure of its neighbors, the cell becoming spherical when the pressure is removed.

In the cytoplasm are suspended the refractive granules or other inclusions, these being frequently in active Brownian movement. In sections the cytoplasm appears finely granular. It may be evenly distributed throughout the cell, or may be gathered into fine, irregular strands forming a network. In cells fixed in osmic acid vapor occur tiny vacuoles representing the spherical granules which are destroyed in the process of preparing paraffin sections. With other fixers it is but rarely that any trace of the spherical granules, which are so conspicuous in the fresh condition, is found in the sections.

The cytoplasmic inclusions are among the most puzzling features of the epithelium. Chief among these are the highly refractive, spherical granules which are found in nearly every cell. Though granules resembling those of the honey-bee occur in the mid-intestinal epithelium of nearly all insects, the information to be found in the literature concerning such granules, is rather meager. In most descriptions of the intestine of various insects, these granules, where mentioned at all, are referred to as secretion granules or fat droplets, with no further discussion. Frenzel (1886) in his work on the mid-intestinal epithelium of a number of insects, including the honey-bee, has described and figured "Sekretkügeln" or "Safttröpfchen" found in the cytoplasm. They have also been noted by Petersen (1912). Koehler (1920) has considered in some detail the nature of certain of these bodies and their possible relation to digestion.

The cytoplasmic inclusions may be divided into several groups: (1) spherical, refractive granules, 1 to 3μ in diameter; (2) very tiny, refractive granules, spherical or somewhat irregular, 0.2 to 0.5μ in diameter; (3) irregular, slightly refractive bodies; (4) faint, non-refractive rods; (5) vacuoles. These groups are considered below:

1. Koehler (1920) in her work on the inclusions of the epithelial cells of the honey-bee's intestine and the related problems of digestion, discussed but one type of inclusion, the spherical, refractive granules measuring 1 to 3μ. These conspicuous bodies are found in greater or less numbers in almost every cell. They have been variously supposed to be secretion granules playing some rôle in digestion (Zander 1911), or reserve food material (Frenzel 1886). Koehler, as a result of various staining reactions and other microchemical tests, concluded that the granules are composed of some calcium compound, probably calcium carbonate, with an outer covering of some organic material. She believed they might indicate an excretion of calcium by the epithelium, or that they might play an important rôle in the neutralization of acids formed in digestion. These bodies may be found in any cell of the epithelium though the regeneration cells contain few or none (Figs. 10-12, 14, 16-23). The number to be found in any cell varies greatly. In some specimens almost every cell in the epithelium is

literally packed with granules, while in others there may be many cells which contain only a few or none at all, as is the case with many secretion cells (Figs. 13, 15).

The granules are perfectly spherical, appear quite homogeneous, and are highly refractive. They are hyaline, appearing under the microscope bluish or greenish by daylight. They greatly resemble droplets of fat. They are distributed throughout the cytoplasm of the cells and are frequently in active Brownian movement, though after standing some time they usually sink to the bottom of the cell, remaining there in a mass. The granules occur mostly as single spheres, though a great many of these are in pairs, clinging together in spite of Brownian movement or of violent currents in the preparation. Granules in such pairs appear slightly flattened at point of contact. This flattening is a refraction phenomenon, and is also seen when two granules accidentally come together, though it strongly suggests a division form, especially in view of the great number of such pairs which even on prolonged observation are almost never seen to become separated. In this connection it may be mentioned that there have been seen on several occasions forms as shown in Figure 27, the granules being elongate with a constriction at the middle. In such granules the material composing the two halves is seen to be continuous. While such forms are very rare in the honey-bee, in another of the Hymenoptera, *Halictus* sp., one specimen of which was examined, similar granules were found, and in nearly every epithelial cell, one to several such double granules were noted. The significance of these forms is not known. Hanging drops of epithelial cells and isolated granules in various solutions and culture media have been observed for periods of days, but no division or multiplication has ever been seen to take place. When the granules are allowed to stand in Locke's or other saline solution, a marked change in appearance usually occurs after a short time. The refractivity becomes somewhat lessened and the granules assume the appearance of hollow spheres containing a clear liquid or other substance (Fig. 29). This appearance is characteristic for the most part of the smaller granules. The outer covering of the larger ones frequently appears to be double (Figs. 28, 30).

The writer's experience confirms that of Koehler as concerns the failure of the granules to stain with most of the common histological stains. However, with Romanowsky stain, employing wet films fixed in osmic acid vapor and hardened in 70 per cent. alcohol, it is almost always possible to obtain preparations in which the granules appear embedded in the blue cytoplasm like perfectly clear, sharply defined vacuoles, containing each a deeply stained, blue-purple body, about half the diameter of the vacuole (Fig. 9). Similar results were obtained

with Giemsa. The staining even in the same mount, is frequently very irregular, for causes not understood. The deeply stained inner body is usually noted in those granules which are contained within an epithelial cell, while those isolated frequently lack the inner body. In general, the inner body retains the stain tenaciously throughout differentiation and dehydration in acetone or alcohol. Very rarely the entire granule stains solidly, or appears unstained in the center with a film of stain over the surface. The inner body is rarely at the center of the granule, but almost always lies touching one side. The problem of the nature of the granules remains unsolved. Nothing whatever is known of the method of their formation. Is the material deposited in this form by the cytoplasm, somewhat as crystals are formed, or does the organic portion of each granule, if such there be, bring about its formation after the fashion of plastids in plant cells? Are such organic portions self-reproducing or is each formed *de novo* by the cytoplasm? These and related questions can be answered only after much further study.

2. In addition to the larger granules just described, are frequently found very tiny refractive granules, spherical or somewhat irregular in shape, and measuring 0.2 to 0.5μ in diameter (Figs. 10, 12, 16-19, 24-26). These closely resemble the larger granules in appearance except for the irregularity in form. Even when irregular, they are approximately spherical. Rod-like forms are not uncommon and groups have been noted in which nearly all the granules were tiny rods, in length approximately one and one-half times the diameter. These small granules occur singly and in pairs. As is to be expected on account of their small size, they are in much more active Brownian movement than the larger granules, and are usually to be found actively dancing about long after the others have sunk to the bottom of the cell. The tiny granules have been considered as being distinct from the larger ones for several reasons, namely: their irregularity of form; the presence of rod-like forms; the fact that they are all of approximately the same diameter, tiny granules frequently being found in cells containing large granules with none intermediate in size; and further, the staining reaction to be mentioned presently.

Since the tiny granules were not considered separately until late in the present study, data obtained regarding their specific reactions are meager. In general their reactions are similar to those of the larger forms in that they are not to be found in sections and do not stain with common histological stains. No change is noticeable in the tiny granules after they have stood in salt solution. With Romanowsky and Giemsa following fixation with osmic acid vapor, they stain solidly and but for the absence of a surrounding vacuole, are indistinguishable from the deeply staining inner body of the larger

granules. In many cases, however, the granules fail to stain at all with this technique. The similarity in staining of the tiny granules and the inner bodies of the larger ones suggests the possibility that the former are the first stages in the formation of the larger granules. If such were the case, presumably these would become surrounded with calcium carbonate or other inorganic material and thus give rise directly to the larger spherical, refractive forms. Direct division of the tiny granules has not been observed, though the occurrence of elongate forms and pairs suggests that this may occur.

3. In a number of specimens taken from a hive in winter quarters, there were observed in addition to the refractive granules, irregular, slightly refractive bodies, measuring 1 to 1.5μ in diameter. While in such specimens these occurred in almost every epithelial cell, only rarely was there more than one in each cell. These irregular bodies could not be distinguished in stained cover-glass preparations or in sections. On account of the limited material further data were not obtained.

4. Toward the close of this study there was noted for the first time in bees taken during the spring from blossoms and from hives of different apiaries, the presence of slender rods in epithelial cells of the ventriculus (Figs. 21-23). These rods measured 0.1 to 0.2μ in diameter by 1 to 2μ in length. They were colorless and not refractive and could be distinguished from the cytaplasm in which they were suspended only with some difficulty. In this respect they resembled somewhat certain spirochaetes. The number to be found in any cell varied greatly. Many contained but very few, in which cases it was easy to observe the individual rods. These frequently exhibited slight Brownian movement. Other cells contained many rods which formed compact masses, usually at the periphery (Fig. 21). In such masses it was difficult to resolve the individuals. Many cells lacked these bodies, though they could be found in nearly all bees after prolonged search. In addition to the rods the refractive granules were present in apparently normal manner. Repeated efforts to stain the rods with Romanowsky, Giemsa and hematoxylin failed completely, not the slightest trace of them being found after staining, either in cover-glass preparations or in sections. The possibility that these bodies are needle-like crystals is not precluded.

5. Occasionally there are noted one to many spherical vacuo'es in epithelial cells. They appear to consist of a liquid which is colorless or at times shows traces of pink. When present there are usually one to several vacuoles, about one-fifth the diameter of the cell. Rarely the cell is completely filled with small vacuoles. These are not to be confused with those surrounding the planonts of *Nosema apis* since no bodies can be made out within the vacuoles, either in fresh or

stained preparations. Since vacuoles have been observed more frequently and in greater numbers in bees from colonies suffering from various disorders, than in healthy bees, it is possible that the vacuoles indicate a pathological condition.

From the scope of the present study, the foregoing survey of the histology and cytology of the honey-bee's ventriculus has necessarily been in some respects a catalogue, rather than a discussion, of the many structures concerned. Their consideration has necessarily been almost entirely from the morphological point of view, and even in this respect much remains yet to be done, while the many related physiological problems, the solution of which is vital to an understanding of the whole subject, remain a practically unexplored field.

THE RELATION OF CYTOPLASMIC INCLUSIONS TO INTRACELLULAR MICRO-ORGANISMS

It is seen from the foregoing that in the cytoplasm of the epithelial cells are found a number of different bodies, of the nature, origin, behavior and ultimate fate of which it is not possible at this time to give a satisfactory explanation. A cursory examination of insect tissues in general reveals the fact that granules or other inclusions are characteristic not alone of the epithelial cells of the honey-bee's midintestine, but indeed of nearly every tissue of every insect. The same is true for many other arthropods. The further study of these inclusions becomes of immediate importance when the common occurrence in insects of intracellular parasites and symbionts is considered.

Intracellular parasitism in insects is of such common occurrence as to constitute an almost universal phenomenon. Many such parasites possess complicated life cycles and our knowledge of many is but fragmentary. Furthermore, in a number of cases in which organisms pathogenic for vertebrates pass a portion of their life cycle in the tissues of insects or arachnids, no trace of the organism has been found in the arthropod host. It is conceivable that the forms assumed by the organism in the arthropod tissues so closely resemble granules or other normal inclusions, and are thus so thoroughly masked, that they easily escape detection. That this may well be the case is borne out by the history of Rocky Mountain spotted fever, a tick-borne disease in which the causal agent is transmitted through many generations of ticks via the egg. The organism (one related to the Rickettsia group) has only recently been discovered by Wolbach (1919). He has described three forms of the organism in the tick, namely, tiny rods in the digestive tract, and two forms of short, paired rods or cocci in various tissues, one form being intranuclear. These organisms stain only with Giemsa. In another tick-borne disease, Texas cattle fever, in which the organism is transmitted via the egg to the second gen-

eration of ticks, the form present in the tick has not been described, although the form in the vertebrate host is well known. In certain tick-borne spirochaetoses there have been described or suspected granule stages of the organism in the tick (Leishman 1910, African relapsing fever; Balfour 1911, 1912, Hindle 1911, spirochaetoses of fowls. Marchoux and Couvy (1913) dissented from Hindle's view, claiming the granules found in ticks to be normal and not derived from spirochaetes.) The literature of Rickettsia in connection with typhus and trench fever, transmitted by lice, is suggestive. These organisms were held by several investigators to be merely normal granules (Wolbach, Todd and Palfrey 1922, bibliography). Tiny granule-like organisms of the Rickettsia type, both intra- and extra-cellular, some transmitted hereditarily, have been found in more than a dozen insects and ticks, and are apparently of general distribution throughout these groups. In his work on the etiology of yellow fever, Noguchi (1919) discovered that in one culture of the causal organism, *Leptospira icteroides,* the typical spiral form had disappeared, while in its place were many tiny granules. The spiral form was later recovered in transfers from this culture. Noguchi suggested that the organism may possess a granule stage in its life history—an especially interesting possibility in view of the fact that the disease is carried by an insect and the further fact that the form present in the insect has not yet been described. The few examples cited will serve to show that in many instances organisms in the tissues of insects can be recognized as such only with difficulty or not at all, and that as a result the many cell inclusions must be studied carefully and in some cases are rightfully to be placed under suspicion.

The problem is further complicated by the common occurrence of intracellular symbionts, certain organisms being constantly present in definite regions or organs or cells of various species of insects. These organisms are transmitted from generation to generation through the egg, and their development in the embryo and adult follows a course as definite as that of any organ of the insect itself (Buchner 1912, 1921, bibliography). Since in the species concerned there are no uninfected individuals for comparison, many symbionts now well known and easily recognized, were for some time believed to be merely cell inclusions. This view, for example, was held concerning the large, rod-shaped bacteroids of the Blattidae. The extent to which intracellular organisms have been overlooked and misinterpreted, and the probability that many symbionts or parasites of the granule-like Rickettsia type are yet to be described, make necessary great caution in passing judgment on the cytoplasmic inclusions of insect tissues.

Koehler (1920) considered the possibility of the refractive granules being symbionts, but abandoned the idea on finding them, as she

believed, to be composed almost entirely of calcium carbonate. There
may be noted, however, a number of cases in which symbionts are
found in the epithelium of the mid-intestine of other insects, notably
the bacteroids of the carpenter ant, Camponotus, and yeast-like organ-
isms in the "drug-store" beetle, *Sitodrepa panicea* (Buchner 1912),
the pith-eating Lepidopterous larva, *Nonagria typhae* (Portier 1911),
and certain of the pupiparous Diptera such as Glossina and Melophagus
(Roubaud 1919). There has not been described any organism living
in symbiosis with the honey-bee.

THE VENTRICULUS INFECTED WITH *NOSEMA APIS*

In this study of *Nosema apis* the chief purpose has been the deter-
mination of changes produced by the parasite in the host tissues,
rather than a study of the parasite itself. A consideration of the latter,
however, is a necessary prelude to a study of the pathological histology
of the host. In the literature of the Microsporidian parasites found
in honey-bees throughout the world, the organisms have in nearly all
cases been identified as *Nosema apis* Zander. As noted below, there
is strong probability that at least one other Microsporidian species may
be present. Identification at best is somewhat uncertain because of
the technical difficulties in determining accurately all the different
stages in the life cycle, and further because of the conflicting accounts
of various writers. The parasite most commonly found in the writer's
material has been provisionally identified as *Nosema apis*.

The morphology and life-history of the parasite have been dis-
cussed in some detail by Zander (1911, 1921) and by Fantham and
Porter (1912a, 1912b), while White (1919) has given much informa-
tion concerning the resistance of the spores to chemical and physical
agents. Kudo (1921) has added some notes concerning the morphology
of the spore of *Nosema apis* and has recorded the occasional occur-
rence of an undetermined Microsporidian, possibly a new species of
Nosema, in the ventriculus of the honey-bee.

The morphology and development of *Nosema apis* as described by
Zander and Fantham and Porter, which is very similar to that given
by Stempell (1909) for *Nosema bombycis* Nägeli, is reviewed below,
together with observations of the writer.

The spore of *Nosema apis* is swallowed by the bee with food or
water and enters the mid-intestine. Here the spore germinates, this
process consisting of the discharge of the coiled polar filament through
a pore at one end of the spore, followed by the issuance of the ameboid
germ. According to Fantham and Porter this body contains two
nuclei which appear as refractive spots. Each amebula gives rise to
one or sometimes two uninucleate bodies, termed planonts, which move
slowly about by means of pseudopodia. These may multiply in the

lumen of the intestine, giving rise to colonies of young planonts, "each of which moves about over the epithelial surface of the gut, and finally penetrates between the cells or directly enters them and becomes intracellular. . . . The method of penetration of a cell by a planont is most difficult of observation, though it has been seen in life on a few occasions." Unfortunately details of the actual process of penetration were not given. Neither Zander nor Fantham and Porter have taken into consideration the peritrophic membranes or the striated border in considering the movements of the planonts from the germinating spore to the penetration of the epithelial cells. Presumably the spores after they enter the intestine are contained within the innermost peritrophic membrane and are thus separated from the epithelium by several layers of these membranes. The latter are for the most part effective barriers to bacteria and food materials, and the method by which the planont penetrates them is not clear. Fantham and Porter stated that the planonts free in the lumen "stain fairly well with Romanowsky stains" but only moderately after they have become intracellular, and are distinguishable from the cell contents only with some difficulty. These investigators were able to distinguish planonts from other organisms such as yeasts "(1) by their movements, (2) the stainability of the nucleus, (3) by chemical tests, of which that for fungus cellulose is the chief. Planonts have no fungus cellulose." In addition to penetrating epithelial cells directly from the lumen, the planonts "may reach the haemocoel or body cavity of the bee and remain there in a resting condition for some time. They lose their motility temporarily, become rounded or oval and lie quiescent. After an interval their activity returns and from the haemocoel they retreat between the cells to the epithelium of the gut, which they gradually penetrate." These investigators found planonts and meronts in the blood of the bee, but their evidence for the return of the planont from the haemocoel to the epithelium, involving a second penetration of a well developed, chitinous basement membrane, was not indicated. White (1919) stated that "in infecting the stomach the parasite reaches the basement membrane but does not penetrate it."

Arrived within an epithelial cell "the active motile planont becomes passive, loses its pseudopodia and enters on a growing stage," which is followed by multiplication after a short time (Fantham and Porter). The parasite at this stage is known as a meront. The round or oval, uninucleate meront increases in size and divides most commonly by binary fission, though there may be produced chains of daughter meronts or large multinucleate meronts which later divide into typical meronts. In Zander's (1921) diagram and microphotographs, the meront stage is represented by "nests" of greatly elongate forms or

chains of as many as eleven individuals, the isolated oval forms being greatly in the minority. Elongate forms were not common and chains were not observed at all in the writer's material.

In distinguishing the planonts and meronts from normal cell inclusions the appearance of the parasites in the fresh condition is a particularly important consideration. Fantham and Porter stated that the planonts after they have become intracellular are very difficult to see either fresh or stained. Stempell (1909) found the same to be true of the planonts of *Nosema bombycis*. In the writer's experience the intracellular planont stage has never been made out with absolute certainty. Apparently this form is similar in density, refractivity, etc., to the protoplasm of the cell and stains with the same intensity. Fantham and Porter have not described the appearance of the living meront, though in their figures drawn from fresh preparations, meronts are shown as rounded or oval bodies, all with distinct nuclei and with finely granular, or in some cases alveolar, cytoplasm. In the writer's preparations the meronts were mostly spherical or oval, and greatly resembled vacuoles with a slightly refractive outer portion. The protoplasm of the meront was clear, homogeneous and apparently of about the same density as the cytoplasm of the host cell (Figs. 24-26, 33-38). Only very rarely could structures be seen within the meronts, these being interpreted as nuclei of the latter (Figs. 26, 32). Stempell (1909) reported that the meronts of both *Nosema bombycis* and *Thelohania mülleri* possess a pellicle-like outer layer of protoplasm. It is perhaps such a structure which appears as the slightly refractive covering of meronts of *Nosema apis*. The meronts are usually somewhat larger than the mature spores. Greatly enlarged multinucleate meronts as described and figured by Fantham and Porter have not been observed by the writer. Their Figure 47, evidently drawn from a fresh preparation, shows portions of four host cells containing five large multinucleate and two uninucleate meronts. In addition there are oval or elongate bodies of about the size of mature spores, which apparently represent the host nuclei. From the writer's observations the nuclei of the epithelial cells are almost always very much larger than Nosema spores, even the small nuclei of the regenerative cells being usually at least twice as large as the spores. The nuclei frequently appear as large spheres with a number of distinct spherical or somewhat irregular bodies suspended within (Fig. 3), closely resembling the large multinucleate meronts shown by Fantham and Porter. There might, as a result, be a possibility in the examination of fresh material, of mistaking a large meront for the host nucleus, and an abnormally small nucleus for a parasite, and vice versa.

There was occasionally encountered another form of meront which may not be that of *Nosema apis* but may be one stage of the undeter-

mined Microsporidian found by Kudo (1921). These forms were elongate bodies, some of which were constricted at the middle and nearly all of which were bent forming an obtuse angle (Figs. 39-48). The elongate, bent forms were usually highly refractive, resembling in this respect, the mature spore. No internal structure could be made out. The forms undergoing division were somewhat less refractive and usually contained at the constriction a distinct vacuole, which seemed also to be undergoing division (Fig. 48). Shorter forms with a vacuole at one end also occurred, together with short refractive forms without a vacuole, resembling the ordinary mature spore of *Nosema apis*. Whether these are spores or whether they are meronts which later become the refractive elongate and dividing forms with vacuoles, could not be determined from the limited material. Accompanying the forms just described were occasionally numbers of mature spores which were refractive and contained a large vacuole at one end, similar in this respect to the spores of Kudo's Microsporidian. That these forms, both meronts and spores, are distinct from *Nosema apis* is indicated by a characteristic staining reaction. With the Romanowsky stain used by the writer, the meronts and spores of *Nosema apis* stain blue with rarely any trace of red. On the other hand, the vacuolate forms contain a more or less irregular group of ruby-red granules within the vacuole. Infection by this form was almost always accompanied by infection with *Nosema apis*, small scattered areas being occupied by the vacuolate parasites. In one series of sections, for example, the epithelial cells were all heavily infected with *Nosema apis*, while one Malpighian tube contained exclusively forms with the brilliant red granules.

Following multiplication of the meronts within the cell, spore formation takes place. This process has been described in some detail by Fantham and Porter. Each ultimate meront undergoes a number of somewhat complex cytoplasmic and nuclear changes, resulting in the formation of a single spore with several nuclei and a polar capsule containing a long coiled thread, the polar filament, the whole being provided with a dense, refractive spore wall. Fantham and Porter stated that "when young the contents of the spores are finely granular and a single nucleus can be seen within them in life." Such forms have not been seen in the writer's preparations. The protoplasm of young spores is denser than that of meronts and appears homogeneous throughout except for the frequent occurrence of a vacuole at one or both ends as described by Fantham and Porter. At this stage there are discernible at times several cross striations in the protoplasm of both fresh and stained spores. According to both Zander and Fantham and Porter, these may represent the polar filament in process of formation. The vacuoles and cross striations are more marked after

the spores have remained some time in salt solution. In older and mature spores, the formation of the refractive spore wall makes examination of structural details impossible in the fresh condition. Fantham and Porter's detailed description of the structure of the mature spore differs in many important respects from that of Kudo (1921). The former represent the spore as containing a binucleate, girdle-like sporoplasm at the equator of the spore, surrounding the polar capsule with its coiled polar filament. There are in addition three accessory nuclei. Kudo's diagram shows a uninucleate, rounded sporoplasm at one end of the spore, the polar capsule being at the other end, with no accessory nuclei. It may be mentioned that with ordinary histological technique these details cannot be made out at all. The spores stain as shown in Figure 4, there being a clear space at one end, traversed by an axial thread, probably the base of the polar filament. The remainder of the spore contents, including probably the polar filament, forms a deeply staining, elongate triangular mass.

Spores contained in epithelial cells which are discharged into the lumen of the intestine, are eventually voided with the feces and may then serve to infect bees taking food or water thus contaminated. To what extent reinfection by parasites produced within the same ventriculus may take place, has not been determined. Fantham and Porter (1912b) believed this to be possible to a limited extent by means of mature spores. Zander (1921) believed that reinfection may take place by means of younger stages as well as spores discharged into the lumen. Maassen (1912) held that reinfection by means of mature spores was impossible, though it could probably be brought about by younger forms. Zander held that only by some method of reinfection could be explained the fact that frequently the entire epithelial layer is filled with parasites. This view is supported by a number of facts. It has been the writer's experience that in the summer and early fall the number of infected bees is small. About October or November it is common to find one infected bee in every twenty or thirty, and it is noteworthy that almost without exception such infected bees are very heavily infected, while no traces of parasites can be found in other bees from the same hives. Equal opportunity for ingestion of spores may be assumed for all bees of the same hive. The heavy infection of a few out of many uninfected individuals may be due to differential susceptibility, or to the spread of the parasites within the host following initial infection by relatively few spores. The latter would seem the more probable, and is borne out by the occurrence of areas parasitized exclusively by the undetermined Microsporidian, surrounded by areas containing only *Nosema apis*.

All accounts agree that infection with Nosema is most frequently found in workers, though drones and queens are susceptible. How-

ever, the drones and queens of even heavily infected colonies may escape infection altogether. As to the larvae, reports differ. White (1919) as a result of inoculation experiments concluded that the larvae are not susceptible. Fantham and Porter (1912b), however, reported finding meronts and occasionally spores in cells of the larval mid-intestine, and Maassen (1919) reported infection of the brood. The infection is usually limited to epithelial cells of the ventriculus, whether of workers, drones or queens, though in heavily infected specimens it is not uncommon to find the parasites within cells of the basal portion of the Malpighian tubes. Fantham and Porter (1912b) have reported the presence of planonts and meronts in the body fluid. Parasites have not been found in cells of the esophageal valve nor in those of the small intestine.

CHANGES IN THE VENTRICULUS PRODUCED BY NOSEMA

The presence of the parasites produces certain changes in the ventriculus which are recognizable with the naked eye. When the cells of the epthelium are filled with spores, the translucent, reddish brown appearance becomes a milky or chalky whiteness. On being crushed under a cover-glass the entire ventriculus may disintegrate forming a milky mass. White (1919) found that "the organ is often increased in size, the circular constrictions are less marked, and the transparency is diminished. In late stages of the disease, however, the stomach approaches the normal in size and the constrictions are again well marked." Swollen forms were not common in the writer's material. It is only in advanced stages of infection, however, that the presence of the parasites can be detected by the milky or chalky appearance, and not always with certainty even then. While normally reddish brown in color, the ventriculus of healthy bees varies from a whitish yellow to dark brown. When the epithelial cells of the lighter colored specimens are filled with large refractive granules, the outward appearance is somewhat similar to that of an infected ventriculus. Microscopic examination is the only certain method of determining the presence or absence of the parasites. The consistency of the ventriculus is markedly different in advanced stages of infection. Normally it is firm and when crushed under a cover-glass tends to recover its form. The peritrophic membranes remain together in a mass. The heavily infected ventriculus has lost its firmness and elasticity and disintegrates readily. Many cells filled with spores remain intact, but an enormous number of spores escape from the easily ruptured cells. Peritrophic membranes are rarely recognizable as such.

Changes in the general shape and arrangement of epithelial cells and other structures due to the presence of Nosema become apparent

only after the organisms have been fairly well distributed throughout the intestine and the majority of cells have become infected. Newly infected cells, except for certain cytoplasmic features, appear to be quite similar to their uninfected neighbors (Fig. 3). Infection may proceed to a stage where the majority of the cells contain a number of meronts, or even spores, before any differences are noted other than the presence of the parasites themselves. This is true of fresh as well as stained tissues. The size and shape of the cell and the appearance of the cytoplasm are unchanged. The striated border and peritrophic membranes are normal. The formation and discharge of secretion cells proceeds as usual. The small, stalked secretion cells which have been budded off from the larger epithelial cells may or may not contain meronts or spores.

After the epitelium has been completely parasitized and the infection has persisted some little time, a number of marked changes are recognizable. The musculature and basement membrane alone are unaffected. The epithelial cells are in general larger, evidenced by their greater length in sections, and increased diameter as seen in fresh preparations. Fantham and Porter (1912b) stated that "the passage of the spores outwards into the lumen of the gut causes tears and gaps to appear in the intestinal wall," such injured cells being replaced by new ones. Liberation of spores in this fashion has not been observed by the writer, the parasites practically always being within host cells until the latter have left the epithelium and have disintegrated in the lumen. These writers further stated that "when an intense infection is present, the bee seems to lose its power of reforming cells." Quite the reverse would seem to be true from the writer's experience. There is a marked tendency toward increased proliferation of cells in heavily infected individuals, resulting in an abnormally thickened epithelium, composed of greatly elongate cells attached to the basement membrane and occasionally there are elongate secretion cells arising from these (Fig. 7). This condition may also be explained by delay in the discharge of secretion cells into the lumen. Excessive proliferation and elongation of cells are by no means invariable accompaniments of heavy infection, nor are they found only in infected tissues. In many infected areas the cells are not at all elongate. Figures 6 and 7 represent different regions of the same section, the cells of one being enormously elongate, while those of the other are quite the reverse, the degree of infection being the same in both. One method of formation of secretion cells is strikingly shown in Figure 7. Small cap-like cells are seen covering the ends of several epithelial cells, the former being entirely free of parasites, while the parent cells are filled with them. This method of secretion-cell

formation, as already described, has also been observed in uninfected specimens, which indicates that even heavily infected cells may function normally in some respects.

In heavily infected areas Fantham and Porter (1912b) found "the secretory epithelium reduced to the condition of a pulp or sponge-like meshwork, enclosing large colonies of meronts and spores within its strands." Degeneration of the cells to this extent has not been noted in the writer's material. With the exception of the region next the basement membrane, the cell outlines are usually clear (Figs. 4-7). The nidi, the cells of which may contain few or no parasites, even in heavily infected individuals, may be little changed or, on the other hand, may not be recognizable at all, as shown in Figures 6 and 7, drawn from different areas of the same section.

With advance in the degree of infection, the striated border becomes less marked. In fresh mounts the epithelial cells filled with spores usually lack the radiating hair-like processes so conspicuous in the case of healthy bees. In sections the hair-like structure may be quite definite in some areas, in others there may be merely a granular mass (Figs. 5-7). Along with the striated border, the peritrophic membranes become more indefinite and their formation more uncertain as infection progresses. Frequently the peritrophic membranes are scarcely recognizable, the lumen of the ventriculus being entirely filled with spores, either free or within discharged cells. In such sections the space between the spores may be occupied by a finely granular substance, together with bacteria and yeasts. Maassen (1919) noted the occurrence of greater numbers of bacteria in infected than in uninfected individuals.

The morphologically recognizable effects of Nosema upon the contents of the epithelial cells are few. The host nuclei appear not to be affected, since in heavily infected cells they are not appreciably different from those of normal cells. Parasites within host nuclei have not been mentioned by the various investigators, nor has this condition been noted by the writer. This point, however, is difficult of determination with certainty, for in many heavily infected cells there are no nuclei. It may be that in such cases the nuclei have been destroyed, or on the other hand, the cells may be secretion cells which never possessed nuclei.

Fantham and Porter (1912b) found a clear space or "halo" surrounding meronts a short time after they had become intracellular, this halo becoming more marked with the growth of the meront. These writers considered the clear space to be possibly an alteration of the concentration of the liquid surrounding the parasite, due perhaps to the protoplasm having been digested by the parasite, or "to the removal by simple absorption from the cytoplasm of the invaded

cell of various granular constituents, used by the parasite as food." It is not clear whether the "granular constituents" refer to the conspicuous cell inclusions, or to the protoplasm itself which is at times indistinctly finely granular. Clear spaces or vacuoles surrounding the meronts have been observed but rarely by the writer in fresh material, though in sections a rather definite space may be found surrounding each parasite (Fig. 4). Both Zander (1921) and Fantham and Porter (1912b) have figured "nests" of meronts lying within large clear spaces.

The effect of *Nosema apis* on the various cell inclusions has received little attention. Fantham and Porter have not mentioned these bodies specifically, nor do the latter appear in their figures drawn from fresh preparations, though large numbers of the refractive, spherical granules appear in certain of their microphotographs (1912a). Zander (1921) gave a figure of a healthy cell filled with "Kalkkörperchen" or refractive granules, and showed a few of these in a cell filled with spores. Koehler (1920), who was led to the investigation of the epithelial inclusions in connection with a study of Nosema-infected bees, stated that in cells filled with spores the "calcium-granules" are few or have disappeared altogether. She suggested that the pathological effect of the parasite, while it might be the effect of toxins, might also be due to a disturbance of digestion and resorption resulting from a deficiency in calcium. On testing for calcium in the spore walls, Koehler obtained only negative results, so that apparently the calcium of the granules is not used directly by the parasites. However, she considered the disturbance of the calcium cycle a probability.

The writer's observations agree with those of Koehler as to the decrease in number of the refractive granules in heavily infected cells. It is only rarely, however, that the larger, nucleate cells lack these entirely, though the smaller secretion cells are often without granules. There is no change in appearance or staining reaction of these granules, though a few abnormal forms have been noted (Fig. 31). There is, however, in nearly all cases a very marked increase in the number of the very tiny granules described above (p. 123). These are spherical, slightly irregular or rod-shaped, and very frequently in pairs. In infected specimens it often happens that such tiny granules predominate even in cells which contain no parasites. With Romanowsky these tiny bodies may stain deeply, though quite as frequently they are not to be found after staining, or else their numbers are greatly reduced. Whether these tiny granules represent the central portion of the larger, refractive granules minus their inorganic outer portion, and are thus a degeneration stage of the latter, cannot be stated. It would seem certain, however, that their marked increase

in number is due in some way to the presence of the parasites. The appearance of the cytoplasm is unchanged, though it is, of course, ultimately replaced in large measure by the parasites. The slender, non-refractive rods (p. 124) have been observed in the epithelial cells of a few heavily infected individuals.

SUMMARY OF PATHOLOGICAL CONDITIONS ASSOCIATED WITH NOSEMA

From the foregoing it is seen that throughout infection the epithelial cells retain their identity, the cells not being "destroyed" at all, strictly speaking, since they disintegrate only after they have reached the lumen. Though the cytoplasm is largely replaced by parasites, the nuclei and cell membranes seem uninjured, though the latter are probably more easily ruptured. Along with destruction of the cytoplasm, changes in relative numbers of various cell inclusions take place. There appears a tendency toward increased proliferation of epithelial cells, with consequent thickening of the epithelium. With the advance in infection, the formation of striated border and peritrophic membrane becomes seriously deranged. Changes in the appearance and contents of the organ harboring the parasites occur only with heavy infection. The color changes from red or brown to chalky white, and the firmness and elasticity of the tissues are lost.

From the behavior of infected bees it is seen that these pathological conditions do not immediately produce outward symptoms of disease. In a colony known to harbor the parasites, it is impossible to distinguish from appearance or behavior, the infected from the uninfected individuals, except those actually dying of the disease. Since in this latter condition the usual symptoms, i. e., crawling, inability to fly, distended abdomen, etc., are quite as characteristic of disorders not associated with Nosema, microscopic examination is the only certain method of diagnosis. Since it is thus possible for the infection to be in an advanced stage without having any apparent effect on the behavior of the bee, the ultimate pathological effect, namely, the weakening and death of the bee, would appear to be due, not to any one of the pathological conditions enumerated above, but to the collective and cumulative effect of some or all of them. Toxins produced by the parasite, if any, would seem to make little or no contribution to the pathological condition, since their effects could be expected to manifest themselves during the growing stages of the parasite. Until more is known of the physiology of the honey-bee and of insects in general, the most plausible explanation of the condition, and the one commonly advanced, is that some derangement of the digestive processes takes place, which leads to the malnutrition and hence the weakening and ultimate death of the host.

A PATHOLOGICAL CONDITION OF THE VENTRICULUS NOT ASSOCIATED WITH NOSEMA

In June 1920 there came to the notice of the writer a hive which had been suffering a marked and constant loss of bees since it was set out in the spring. There were generally to be found on the ground near the hive as many as a hundred or more bees which were in great distress, crawling about excitedly or sluggishly, or lying motionless except for occasional trembling movements of wings and legs. Examination failed to reveal the presence of Nosema and there was no apparent cause for the death of the bees in such numbers. The colony was an isolated one, located in the residential district of St. Anthony Park, St. Paul, about one-quarter of a mile from the apiary at University Farm. No marked loss of bees was noted in the latter apiary.

The mid-intestines of the diseased bees examined in June 1920 were mostly pale yellowish, and decidedly smaller in size than normal. The contents were colorless or pale brown. The hind-intestine had a pale, watery appearance. When the ventriculus was crushed under a cover-glass, the epithelial cells which became detached lacked the elasticity of normal cells. They tended to retain the elongate-pyriform shape instead of becoming spherical when the pressure of adjoining cells was released. Apparently normal granules were present in the cells, though in some specimens there were in addition refractive spheres or globules, possibly of some liquid, very much larger than the ordinary refractive granules. Sections revealed a rather striking pathological condition, totally unlike that encountered in Nosema-infected bees. The entire cellular structure had in many regions become a coarsely granular mass. The outlines of many cells and nuclei were wholly indefinite (Fig. 8). In certain regions there appeared to have taken place an excessive and irregular proliferation of cells, the mass of discharged cells forming a layer thicker than the epithelium itself. Parts of the epithelium seemed to have been shed into the lumen *en masse,* the more or less intact epithelial layer being separated from the basement membrane by a considerable area filled with coarse, deeply staining granules. In certain cases, as shown in Figure 8, the epithelium had been given off in a body, but a new epithelium had been formed beneath the old. As a result there were two layers of epithelium, both showing the degenerate, granular condition. The inner layer was broken or had completely degenerated in several places, but portions of the striated border were present together with a peritrophic membrane in process of formation, and several of the latter in the lumen completely formed. On the surface of the layer resting on the basement membrane, was an unbroken striated border with the beginning of a peritrophic membrane. The basal por-

tion of this epithelial layer had lost all trace of cell outlines, being a uniformly granular area. The Malpighian tubes and muscle fibers surrounding the ventriculus were also degenerate.

Further examination of bees from this colony was not made in the season of 1920, though the owner stated that the loss of bees continued to a certain extent throughout the entire summer. The colony yielded little or no surplus honey, but was able to winter over. Shortly after it was set out in the spring of 1921 a similar loss of bees was noted. The number of stricken bees to be found at any one time, however, was rarely over forty or fifty and at times not more than a dozen. On examination the ventriculus was found to be pale and translucent, with a dark mass at the posterior end formed by the contents. The ventriculus was usually of less than normal size and was frequently of uneven diameter. Within the epithelial cells were found large numbers of the non-refractive, slender rods described above (p. 124). Since these rods were also found in healthy bees from other apiaries, no pathological significance was attached to them. In addition there were noted the abnormally large refractive bodies found the previous summer, and also a number of vacuoles. One apparently healthy bee, taken from the entrance, was heavily infected with *Nosema apis*. This parasite was not found in any other individuals, whether active or crawling. In the few specimens sectioned, the striking pathological condition found the previous season was not apparent. The only abnormal structures noted were occasional large spheres, staining lightly but uniformly with eosin. The loss of bees continued until shortly after July 1, 1921, about which time the colony was requeened.

The cause of this pathological condition, and whether or not it is infectious, are not known. It is merely one more example of the many disorders of the adult honey-bee which cannot be distinguished from each other with certainty until our knowledge of insect physiology, and of the normal and pathological histology, not alone of the mid-intestine, but of all other organs as well, is greatly extended.

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EXPLANATION OF FIGURES

Figures 1 to 9 drawn with aid of camera lucida from stained preparations;
Figures 10 and 49 drawn with aid of camera lucida from fresh material.

EXPLANATION OF PLATE IX

1. Normal ventriculus, longi-section. Gilson. x 350.

2. Dividing nucleus of regeneration cell. Gilson. x 790.

3. Cross-section of epithelium, one cell containing meronts of *Nosema apis*.
Vacuoles in cytoplasm represent refractive granules of fresh tissue. Osmic
acid vapor. x 790.

4. Cells containing meronts and spores surrounded by clear areas in cyto-
plasm. Gilson. x 770.

5. Longi-section, junction of heavily infected ventriculus with small intes-
tine; base of Malpighian tube slightly infected. Infected area ends abruptly
with beginning of small intestine. Gilson. x 180.

6. Cross-section, heavily infected ventriculus; shape and arrangement of
cells nearly normal. (Compare with Figure 7). Sublimate-alcohol. x 180.

7. Cross-section, same specimen as Figure 6. Epithelium enormously thick-
ened as result of elongation and increase in number of cells; several cap-like
secretion cells, some with cross-walls; nidi not recognizable as such. x 180.

8. Cross-section, ventriculus; pathological condition not associated with
Nosema. Two epithelial layers apparently due to sloughing and regeneration:
sloughed portion, *A*, nearly intact with striated border and peritrophic mem-
brane; newer epithelial layer, *B*, resting on basement membrane, degenerate but
with striated border and peritrophic membrane forming. Malpighian tube, *m. t.*,
and muscle fibers, *m. f.*, degenerate. Hollande. x 325.

9. Refractive granules from epithelial cell, cover-glass preparation, osmic
acid vapor, Romanowsky stain. Granules appear as vacuoles embedded in blue
cytoplasm, each with blue-purple inner body. x 1120.

PLATE IX

EXPLANATION OF PLATE X

10. Isolated epithelial cell with striated border. The cytoplasm contains large, spherical, refractive granules and tiny, somewhat irregular granules. x. 1910.

11-18. Secretion cells. x 1910.

19, 20. Stalked secretion cells with striated border. x 1910.

21-23 Epithelial cells containing slender, non-refractive rods in addition to normal, refractive granules. Figures 21 and 22, x 1910; Figure 23, x 1810.

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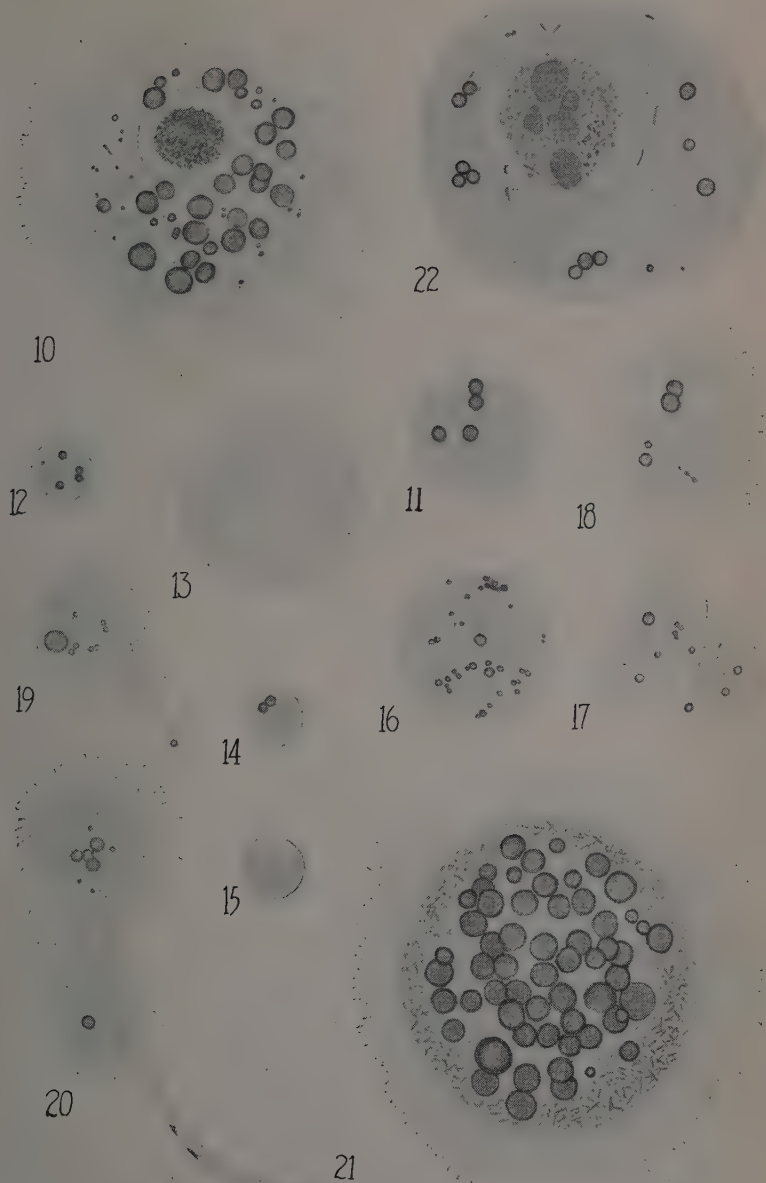
PLATE X

EXPLANATION OF PLATE XI

24, 25. Epithelial cells containing meronts of *Nosema apis* and many tiny, irregular granules. x 1810.

26. Epithelial cells containing spores and meronts, the latter resembling vacuoles. The cytoplasm contains spherical, refractive granules and tiny, irregular granules. x 1810.

27. Double, refractive granule from epithelial cell, suggesting a division form of the spherical, refractive granules. x 1810.

28-30. Refractive granules after standing in Locke's solution one to two hours. x 1810.

31. Abnormal forms of refractive granules from heavily infected epithelial cells. x 1810.

32-38. Young meronts of either *Nosema apis* or undetermined Microsporidian. x 1810.

39-48. Meronts, probably of undetermined Microsporidian. x 1810.

49. Young spore, *Nosema apis*. x 1810.

50. Epithelial cell filled with spores, together with a number of spherical, refractive granules. Microphotograph, fresh preparation. x 890.
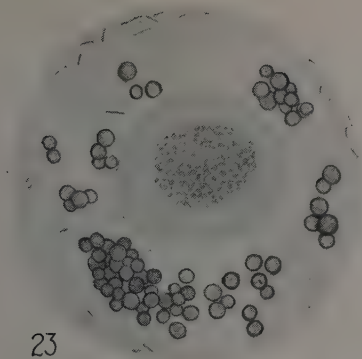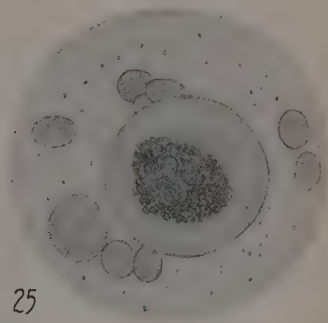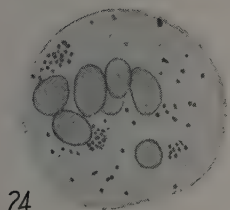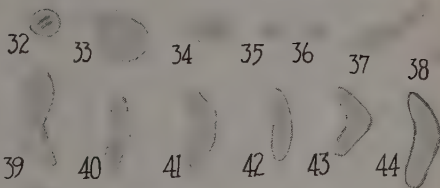
23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50

PLATE XI

The Parasitism of
Colletotrichum lindemuthianum

By J. G. Leach
Division of Plant Pathology and Botany

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The Parasitism of
Colletotrichum lindemuthianum

By J. G. Leach
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CONTENTS

ILLUSTRATIONS

THE PARASITISM OF COLLETOTRICHUM
LINDEMUTHIANUM

By J. G. Leach[1]

INTRODUCTION

It has been a matter of common knowledge for many years that some species and varieties of plants are more resistant than others to certain diseases. The discovery of the causes for these differences in resistance has been the object of numerous investigations, and, while much has been learned, the question is still far from solved. It is quite evident from what is known that no single factor can explain resistance in all cases and it is probable that several factors, working together or independently, may be involved in most cases of disease resistance. It is also obvious that a more thoro knowledge of the factors underlying normal parasitism and of the relations normally existing between host and parasite must be obtained before much progress can be made in the solution of this difficult problem. The investigations reported here constitute the first steps in a study of the parasitism of *Colletotrichum lindemuthianum* (Sac. and Mag.) Bri. and Cav. They were made with the purpose of obtaining information which might be applied to the solution of the general problem of disease resistance in plants.

HISTORICAL

The literature on disease resistance in plants has been so thoroly reviewed by Butler (14) that it will be necessary here only to indicate the trend of the development of our knowledge of the subject. Early workers, basing their conclusions chiefly on observation, often confused disease-escaping and disease-enduring varieties with disease-resistant varieties. Ward (50), Orton (37), and others soon pointed out and clearly distinguished between these phenomena. Further study of the question has demonstrated that true resistance must depend either on some anatomical character of the host tissue or on the physiology of its protoplasm. As an example of the former, Hawkins and Harvey (31) recently have proved that the resistance of the McCormick potato to *Pythium deBaryanum* is due to the thick-

ness of the cell walls of the tuber, which is sufficient to withstand the mechanical pressure exerted by the fungus. Valleau (48) has shown that certain varieties of plums are more resistant to *Sclerotinia cinerea* because the stomata become plugged with masses of small corky cells.

Ward (50), Gibson (30), and Marryat (36), however, proved for several different species of rust fungi that resistance could not be due to anatomical characters of the host as had been claimed for *Puccinia graminis* by Anderson (1) and Cobb (17). On the other hand it was shown to depend on the "physiological reactions of the protoplasm of the fungus and of the cells of the host."

Resistance to certain fungous parasites has been correlated with a greater degree of acidity of the sap of host plant tissues. Averna-Sacca (4) found that the resistance of grapes to species of Oidium and Peronospora was correlated with a relatively high acidity of the cell sap.

Comes (18) has correlated the rust-resistance of Rieti wheat with a high acid and low sugar content of the sap. With the discovery by Stakman and his co-workers (43, 46) of the numerous biologic forms of stem rust (*Puccinia graminis*) attacking wheat it became very evident that the degree of acidity of the cell sap can not explain all the facts of resistance to this rust. The writer (34) pointed out in an earlier paper that the factors responsible for the resistance to the biologic forms of stem rust of wheat must be specific in relation to each form of rust, and suggested a tentative hypothesis based on a possible specific food requirement on the part of the fungus and a corresponding specific food substance within the host. It was very difficult to secure any direct evidence for or against this hypothesis, as we were unable to culture the rust fungi on artificial media. For further work on the subject it was desirable to secure a fungus, specialized in its relation to host varieties and at the same time capable of growth on artificial media. Since *Colletotrichum lindemuthianum* appeared to meet these requirements, it was selected for study.

Colletotrichum lindemuthianum, the fungus causing the pod spot or anthracnose of beans, was first observed in Popplesdorf, Germany, in 1875, by Lindemuth. It was described by Saccardo and Magnus (38) and named *Gloeosporium lindemuthianum*. A few years later Briosi and Cavara (8) discovered the presence of setae and changed the generic name to Colletotrichum. Since that time the fungus has been the subject of numerous investigations, most of which have dealt principally with its life history and control. Barrus (5), however, in 1911 reported the discovery of strains of the fungus which differed in their ability to attack certain varieties of beans. Edgerton and Moreland in 1916 (27) reported the results of inoculation experiments

with eleven collections of the fungus, concluding that there were "a number of different strains, affecting bean varieties differently." Barrus, in 1918 (6), published results of additional inoculations with ten collections on 137 varieties of beans, but distinguishes only two biologic forms. In a still more recent publication, Barrus (7) has summarized fully previous literature dealing with this fungus, recording also some additional observations and experiments of his own. This paper and other work treating particular phases of the parasitism of the fungus will be referred to in more detail later.

MATERIALS AND METHODS

All the inoculation experiments reported here were made in the greenhouse on pure-line varieties of field beans (*Phaseolus vulgaris* L.) furnished either by Mr. F. H. Steinmetz of the Division of Agronomy and Farm Management, of the University of Minnesota, or by Dr. J. T. Barrett of the California Agricultural Experiment Station. Fifteen collections of *Colletotrichum lindemuthianum* were used. These were obtained during the summers of 1920 and 1922 from the sources indicated below.

Culture No. 2. From a bean pod collected from the Agronomy plots, University Farm, St. Paul, Minn.

Culture No. 3. Isolated from bean pods obtained from the markets, Minneapolis, Minn.

Culture No. 5. From a bean pod collected from a market garden, Duluth, Minn.

Culture No. 6. From a bean pod collected from a garden on the University of Minnesota Fruit Breeding Farm Excelsior, Minn.

Culture No. 7. Obtained from the University of Minnesota mycological herbarium, originally obtained from Dr. G. H. Coons, Michigan Agricultural College East Lansing, Mich.

Culture No. 9. Obtained from the University of Minnesota mycological herbarium, originally collected at University Farm, St. Paul, November, 1919, by F. J. MacInnes.

Culture No. 10. From a bean pod collected from a garden at Grand Rapids, Minn.

Culture No. 12. From diseased bean pods sent by Dr. W. D. Valleau from Lexington, Ky.

Culture No. 15. From a naturally infected bean seedling in the Plant Pathology Greenhouse, University Farm, St. Paul.

Culture No. 16. From bean pods collected in the Plant Pathology plots, University Farm, St. Paul, 1922.

Culture No. 18. From bean pods from the Minneapolis markets, 1922.

Culture No. 19. Furnished by Dr. C. W. Edgerton, Baton Rouge, La., 1922.

Culture No. 20. From bean pods from the Minneapolis markets, 1922.

Culture No. 22. Isolated from infected pods furnished by Dr. M. F. Barrus, Ithaca, N. Y.

Culture No. 25. Culture obtained from "Centralstelle für Pilzkulturen," Baarn, Nederland.

Before comparative inoculations were made, single-spore cultures were started by picking up single spores with a platinum needle from poured agar plates. Stock cultures were grown on green-bean agar and on sterilized bean pods. These were kept either at room temperature or in an incubator at from 20° to 25° C. The fungus rarely formed spores on the agar but it fruited abundantly on the bean pods.

Inoculation was effected by atomizing the plants thoroly with a suspension of spores obtained by washing a sporulating bean-pod culture in from 50 to 100 cc. of distilled water. The inoculated plants were then kept in a moist chamber for 48 hours, after which they were removed and placed on a bench.

Signs of infection appeared in from four to six days, depending upon the age of the plant. Notes were taken, whenever possible, ten days after inoculation. Since the age of the plant has a marked effect on the symptoms, as will be pointed out in more detail later, plants of approximately the same age were used in all comparative inoculations. Any differences in age were taken into consideration in taking notes.

The first series of inoculations was made with Culture 2 on sixty-nine varieties of beans. Various degrees of resistance and susceptibility appeared. A brief description of these symptoms with the symbols used in recording them is given below. Representative types also are illustrated in Plate I, Figure 1.

TYPES OF ANTHRACNOSE INFECTION PRODUCED BY ARTIFICIAL INOCULATION ON BEAN SEEDLINGS IN THE GREENHOUSE

Susceptible (S)...
- S+ Plants wilt and fall over in from 5 to 6 days with profuse and extensive production of acervuli. Red color may be entirely lacking.
- S Large sunken reddish-brown lesions, numerous acervuli.
- S— Small to medium, slightly sunken reddish-brown lesions, few or no acervuli.

Resistant (R)....
- R Small to very small, slightly sunken reddish-brown lesions, no acervuli.
- R— Extremely small reddish-brown lesions, no acervuli.

No immune plants were found; very small lesions were produced on the most resistant.

TABLE I

Effect of Age of Host on Susceptibility to *Colletotrichum lindemuthianum*

Variety No.	Age in days from time of planting	Stage of development at time of inoculation	Results of inoculation
20*	11	Just emerged	Complete susceptibility throughout.
21†	11	Just emerged	Highly resistant throughout, numerous minute brown lesions.
20	18	Second pair of leaves unfolding	Complete susceptibility from cotyledons upward, numerous small lesions on hypocotyl. (See Plate I, Fig. 3)
21	18	Second pair of leaves unfolding	Highly resistant throughout, numerous minute brown lesions.
20	27	Third pair of leaves unfolding	Susceptible only on upper node above second pair of leaves, small to minute lesions below.
21	27	Third pair of leaves unfolding	Highly resistant throughout, numerous minute brown lesions.
20	35	Blossoms not open	Susceptible on very young tissue only.
21	35	Blossoms not open	Highly resistant throughout, numerous minute brown lesions.
20	53	In full blossom	Susceptible on very young tissue only.
21	53	In full blossom	Highly resistant throughout, numerous minute brown lesions.
20	67	Bearing several small immature pods	Young pods badly affected, rest of plant free from large lesions.
21	67	Bearing several small immature pods	Highly resistant throughout, numerous minute brown lesions.
20	83	Bearing both old and young pods	Young pods badly affected, small lesions on older ones.
21	83	Bearing both old and young pods	Highly resistant throughout, numerous minute brown lesions.

*20—Large Garapata, Minn., Selection 119.
†21—Ruby Horticultural Bush, Minn. Selection 3 B-18.

EFFECT OF AGE ON SYMPTOMS

It was soon observed that the age of the plant influenced greatly the type of lesions produced. Old plants, as well as the old tissue of comparatively young plants, appeared to be more resistant than younger tissue or younger plants. All types of symptoms, from complete wilting of most of the plant to very small lesions, were produced on certain plants. The severity of infection in all cases, however, was inversely proportional to the age and hardness of the tissue. In order more carefully to verify these observations, two varieties, 20 and 21, susceptible and highly resistant respectively to Culture 15, were planted at intervals of several days. These were then inoculated at the same time with Culture 15. The results of this inoculation are given in Table I. Plate I (Figs. 2 and 3) illustrates the effect of the age of tissues on the types of lesions produced in this experiment.

These results show very clearly that the age of the tissue involved determines largely the type of lesions produced on a susceptible variety. A resistant variety, however, is resistant regardless of the age of the tissue. It should be stated here that the resistant variety (Ruby Horticultural Bush, Minn. Selection 3 B-18), used in this experiment is very susceptible to Culture 5 as illustrated in Plate II, Figure 1. Whenever there was any doubt as to the resistance of a variety, the inoculation was repeated, using very young plants. In this way error due to the age factor was eliminated. The reasons for this effect of age on the development of the disease will be discussed in more detail later.

BIOLOGIC FORMS OF THE FUNGUS

From the varieties inoculated with Culture 2, nine susceptible and seven resistant ones were selected for use as differential hosts. On these, comparative inoculations were made with the remaining fourteen cultures. The results are summarized in Table II.

An analysis of the data in Table II shows clearly that there are at least eight different biologic forms among the fifteen cultures tested. For convenience those cultures which react in the same way toward all the differential hosts have been grouped together. It will be seen that some of the biologic forms differ in their reaction on as many as ten of the sixteen differential hosts, while a few react differently on only one or two hosts. These differences are marked and distinct and are deemed sufficient for designating the cultures as separate biologic forms. Barrus (6, p. 597) presented similar data from his inoculation experiments but concludes, "that we must regard each of these several cultures as similar either to A or to B and that we have been concerned here with only two strains of the pathogene."

TABLE II
Infection Capabilities of Fifteen Collections of *Colletotrichum lindemuthianum* on Sixteen Differential Hosts*

Host Acc. No.	Variety inoculated	Biologic form Culture No.	I 2	II 3	II 5	II 19	III 6	III 7	IV 10	IV 12	IV 15	V 9	V 22	VI 16	VI 18	VII 20	VIII 25
2	Brown Swedish	Minn. Selection 132	S. 2- 8	S. 2-20	S. 5-55	S. 1- 5	S. 2-30	S. 1- 6	S. 4-27	S. 1- 5	S. 3-24	R. 1-10	R. 2-11	S. 1- 4	S. 1- 4	S. 1- 3	S. 2- 7
65	Navy type	Minn. Selection 69	S. 1- 7	S. 1- 7	S. 1- 1	S. 1- 4	S. 1-11	S 1- 5			S. 1- 5	S. 1- 7	S. 2- 6	S. 1- 3	S. 1- 4	S. 1- 4	R. 2- 8
28	Red Kidney	Minn. Selection 156	S. 2-16		S. 5-61	S. 1- 5	S. 1- 9	R. 1- 6	R. 1- 5	R. 1- 6	R. 4-26	R. 1-10	R. 2-12	S. 1- 3	S. 1- 5	S. 1- 4	S. 2-15
16	Red Indian	Minn. Selection 1101	S. 2-12	R. 1- 8	R. 4-55	R. 1- 5	R. 2-18	S. 1- 6	S. 2-15	S. 1- 4	S. 3-24	S. 1-12	S. 2-13	R. 1- 4		R. 1- 5	R. 2-11
12	Navy type	Minn. Selection 1083	R. 3-27	R. 1- 6	R. 4-19	R. 1- 4	S. 2-10	S. 1- 5	S. 1- 1	S. 1- 6	S. 1- 3	S. 1- 8	S. 1-22	S. 1- 5	S. 1- 3	S. 1- 5	R. 2-11
14	Ruby Horticultural Bush	Minn. Selection 98	S. 3-28	S. 1-10	S. 3-22	S: 5- 5	S. 2-22	R. 1- 6	R. 1- 5	R. 1- 6	R. 1- 5	R. 1- 9	R. 2-12	R. 1- 3		R. 1- 3	S. 2-12
15	Improved Yellow Eye	Minn. Selection 1096	S. 3-21	S. 1-12	S. 1- 2	S. 1- 2	R. 4-18	R. 1- 6	R.2- 8	R. 1- 6	R. 1- 1	R. 1- 8	R. 2- 7	S. 1- 3	S. 1- 5	R. 1- 6	S. 2-11
3	Zebra	Minn. Selection 125	R. 2-23	R. 1- 4	R. 5-49	R. 1- 5	R. 2-19	S. 1- 5	S. 3-13	S 1- 6	S. 5-31	S 1- 6	S. 2- 8	R. 1- 4	R. 1- 5	R. 1- 5	R. 2-11
4	Brown Swedish	Minn. Selection 134	R. 2-18	R. 1- 4	R. 5-48	R. 1- 5	R. 2-19	S. 1- 7	S. 1- 6	S. 1- 6	S. 3-23	S. 1- 6	S. 2-19	R. 1- 5	R. 1- 6	R. 1- 5	R. 2-11
7	White Kidney	Minn. Selection 1077	S. 4-19	S. 1- 9	S. 1- 3	S. 1- 3	S. 1- 9		R. 1- 1	R. 1- 5	R. 1-12	R. 1- 6	R. 2-10	S. 1- 3	S. 1- 5	S. 1- 6	S. 2- 8
20	Large Carapata	Minn. Selection 119	R. 2- 9	R. 1- 5	R. 4-29	R. 1- 5	S. 2-13	S. 1- 6	S. 1- 2	S. 1-10	S.10-81	S. 1-10	S. 2-12	R. 1- 3	R. 1- 5	R. 1- 3	R. 2-15
21	Ruby Hort. Bush	Minn. Selection 3 B-18	R. 2-23	S. 1- 9	S. 5-48	S. 1- 4	R. 3-27	R. 1- 4	R. 1- 7	R. 2-16	R.10-92	R. 1- 7	R. 2-16	S. 1- 5	S. 1- 4	S. 1- 5	R. 2-15
27	Improved Goddard	Minn. Selection 1098	S. 2-15	S. 1- 3	S. 5-50	S. 1- 5	S. 2-18	R. 1- 6	R. 1- 5	R. 1- 6	R. 4-29	R. 1- 8	R. 2-13	S. 1- 2	S. 1- 4	S. 1- 3	S. 2-12
43	Long Yellow	Minn. Selection 142	S. 3-38	S. 1- 8	S. 4-38	S. 1- 5	S. 1- 7	S. 1- 7	S. 1- 6	S. 1- 6	S. 1- 5	S. 1- 5	S. 2-24	S. 1- 3	S. 1- 7	S. 1- 4	S. 2-10
80	Pink		R. 1-10	R. 1-10	R.10-124			R. 1- 5									
81	Red Mexican		R. 2-16	S. 1- 6	S. 2-10		R. 2-17		S. 1- 6	S. 1- 6	S. 1- 5						

*R = Resistant, S = Susceptible (See page 7). The first figure following the letter S or R indicates the number of separate inoculations and the second figure indicates the total number of plants inoculated.

The writer does not consider this justifiable, because, if we consider difference in parasitism a sufficient basis for distinguishing biologic forms, a difference can not justly be disregarded even if manifested on one host only. Furthermore, these forms may act differently on many other bean varieties which were not inoculated.

For convenience in distinguishing the different biologic forms, an analytical key has been constructed and is presented as Table III. With the aid of this key, which is of the simple dichotomous type, it can be seen at a glance how any one of the biologic forms differs from the other ones. Also an unknown biologic form may be readily identified by a few simple inoculations.

TABLE III

Analytical Key to Biologic Forms of *Colletotrichum lindemuthianum*

Brown Swedish, Minn. 132, resistant (R)...V
Brown Swedish, Minn. 132, susceptible (S)
  Navy, Minn. 69, resistant...VIII
  Navy, Minn. 69, susceptible
    Red Kidney, Minn. 156, resistant..IV
    Red Kidney, Minn. 156, susceptible
      Red Indian, Minn. 1101, resistant
        Navy, Minn. 1083, resistant...II
        Navy, Minn. 1083, susceptible
          Ruby Hort. Bush, Minn. 98, resistant
            Improved Yellow Eye, Minn. 1096, resistant.............VII
            Improved Yellow Eye, Minn. 1096, susceptible.................VI
          Ruby Hort. Bush, Minn. 98, susceptible.........................III
      Red Indian, Minn. 1101, susceptible...I

MORPHOLOGY OF THE BIOLOGIC FORMS

From the data presented above, it is quite obvious that these biologic forms are distinct entities as indicated by the reactions on differential hosts. It is desirable also to know if there are differences in morphology. Stakman and Piemeisel (43, p. 484-486, 35) have shown that the biologic forms of *Puccinia graminis* Erikss. and Henn. can be distinguished on the basis of spore size if enough spores are measured and if they are produced under normal and uniform conditions. Burger (13) found a great difference in size of spores of several strains of *Colletotrichum gloeosporioides* Penz. The mean spore size in microns for the several strains ranged from 11.54 X 5.52 to 20.34 X 6.45. LaRue and Bartlett (33) also have distinguished on the basis of spore size numerous distinct strains within the species *Pestalozzia guepini* Desm.

A series of comparative spore measurements was made to determine if there were any differences in size of spores of the biologic forms isolated by the writer. Cultures 6 and 15, two forms differing widely in parasitism, were used. The data from these measurements are summarized in Tables II and III. All measurements were made with a No. 6 Leitz objective, using a screw micrometer. With this

combination one space on the rotating drum was equal to 0.25 micron. After several trial measurements it was found that the biometrical mode could readily be determined by measuring one hundred spores for length and fifty for width. The data presented here are based on the measurement of one hundred spores for length and sixty-four for width, with the exception of three cases in which only fifty spores were measured for width.

The comparative spore measurements of the two forms were made as nearly as possible under the same conditions. Thus the spores taken from sterilized bean pods were from two normal cultures of the same age which had been incubated at the same temperature. Also those spores taken from susceptible hosts were from the same variety inoculated the same day and kept in the same greenhouse. It can be seen from an analysis of the data in Tables IV and V that altho there seems to be an appreciable difference in the size of spores produced on sterilized bean pods, this difference does not hold when the spores are taken from susceptible host plants. In fact the relation of size is completely reversed. The spores of Culture 15, which were smaller than those of Culture 6 on sterilized bean pods, were larger than those of Culture 6 when developed on the host plant. The effect of the medium in this case on the modal spore length is graphically illus-trated in Figure 1. The data indicate that the medium has a marked influence on spore size and that the medium does not necessarily affect both strains in the same manner. Burger (13) found the same to be true for certain strains of *C. gloeosporioides.*

TABLE IV
Spore Measurements

Culture No.	Source of spores	Mean length in microns	Standard deviation	Mean width in microns	Standard deviation
15	Sterilized bean pod Room temperature	14.70 ± 0.075	1.12 ± 0.053	6.11 ± 0.036	0.545 ± 0.026
6	Sterilized bean pod Room temperature	15.72 ± 0.077	1.14 ± 0.054	5.58 ± 0.036	0.428 ± 0.025
15	Susceptible host 3-2-22	15.01 ± 0.075	1.26 ± 0.053	6.49 ± 0.057	0.678 ± 0.040
6	Susceptible host 3-2-22	14.89 ± 0.080	1.19 ± 0.056	6.41 ± 0.047	0.562 ± 0.033
15	Green bean agar Room temperature	14.31 ± 0.063	0.95 ± 0.044	6.87 ± 0.055	0.655 ± 0.039
15	Susceptible host 3-6-22	15.44 ± 0.077	1.141 ± 0.054	6.86 ± 0.065	0.776 ± 0.046
51	Green bean agar 13° C	14.63 ± 0.070	1.04 ± 0.050	6.69 ± 0.046	0.550 ± 0.033

TABLE V

CALCULATED DIFFERENCES IN SPORE SIZES UNDER VARIOUS CONDITIONS

Culture No.	Source of spores	Variable factor	Difference in mean length in microns	Difference in mean width in microns	Difference in mean length divided by probable error of the difference	Difference in mean width divided by probable error of the difference
6 and 15	Sterilized bean pod	Fungus	1.02 ± 0.107	0.53 ± 0.050	9.65	10.60
6 and 15	Susceptible host; variety No. 2	Fungus	0.12 ± 0.109	0.08 ± 0.073	1.10	1.23
15	Sterilized bean pod and green bean agar	Medium	0.39 ± 0.097	0.76 ± 0.065	4.00	11.66
15	Green bean agar: Room temperature and 13° C.	Temperature	0.32 ± 0.094	0.18 ± 0.071	3.40	2.53
15	Susceptible host; variety No. 2, 3-2-22, 3-6-22	Theoretically none. An attempt to duplicate conditions	0.43 ± 0.107	0.37 ± 0.086	4.02	4.30
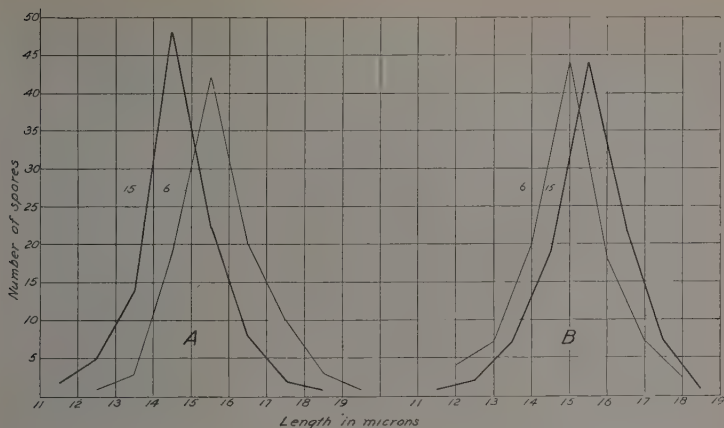
Fig. 1

Influence of Medium on Length of Spores of Two Biologic Forms of *Colletotrichum lindemuthianum*.

    A. Spores grown on a sterilized bean pod.
    B. Spores grown on a living susceptible bean plant.

Since the medium may affect differently the size of spores of different biologic forms, it would appear that, in order to be significant, any differences in spore size must be consistently greater than the variations in size due to the influence of media. It seems, therefore, that the differences in morphology of the two strains measured, as indicated by spore size, are so small and are so readily and specifically influenced by the medium that they are of little or no practical significance.

PHYSIOLOGY OF THE BIOLOGIC FORMS
EFFECT OF TEMPERATURE

Edgerton (26) was the first to study the temperature relations of *C. lindemuthianum*. He found that the fungus was very sensitive to high temperatures. He gave the optimum and maximum temperatures for growth as 22° to 23° C. and 30° to 31° C. respectively. Barrus (7) has recently corroborated Edgerton's results. The minimum, optimum and maximum temperatures were given as 0°, 22° and 34° C. respectively. Edgerton (1. c), altho reporting no differences in temperature relations between biologic forms of *C. lindemuthianum*, was able to distinguish between two biologic forms of *Glomerella cingulata* (Stonem.) S. and V. S., by means of temperature relations. In order to determine if the biologic forms used in this work could be distinguished on the basis of reaction to temperature, a series of tests was made as follows. Petri dishes of uniform size were poured with uniform amounts of the same preparation of green-bean agar. These

were allowed to stand for 48 hours. At the end of this time contaminated plates could be detected and discarded. Duplicate plates were then inoculated in the center with fresh spores of Cultures 5, 6, and 7, taken from sterilized bean pods. The plates were incubated at room temperature for 48 hours before distribution to the various temperatures. The diameter of each colony was measured at the end of ten days. The results of the experiment are illustrated graphically in Figure 2. The differences in the amount of growth made by the three biologic forms at the various temperatures were very slight and evidently fall within the limits of experimental error. The difference in growth of two colonies of the same strain was often much greater than the average difference between the strains. With loosely fitting petri dishes, evaporation from the agar takes place rapidly, and often unevenly, especially at the higher temperatures. The rather low optimum obtained in this experiment can no doubt be accounted for by the drying of the agar near the end of the experiment in the incubator held at 23°. In order to eliminate the factor of uneven evaporation from the agar at the different temperatures, a series was run in which the petri dish cultures were kept in sealed museum jars over dilute
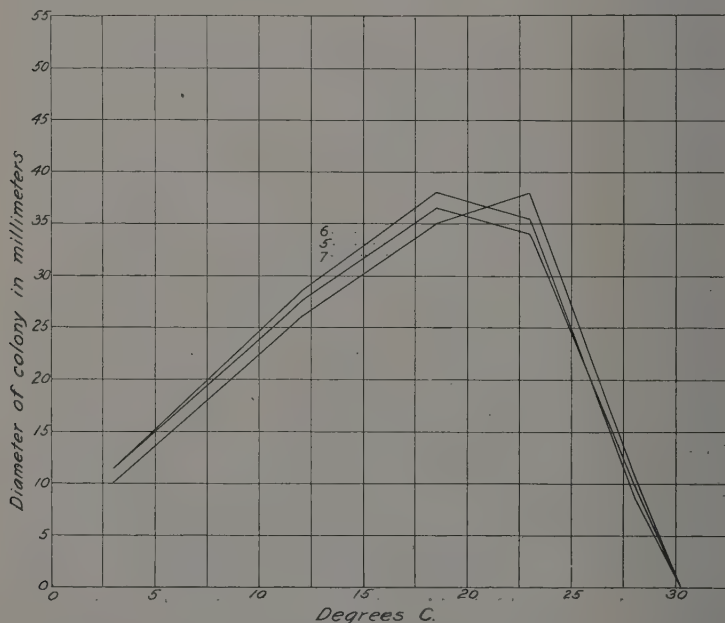

Fig. 2

Influence of Temperature on Growth of Three Biologic Forms of *Colletotrichum lindemuthian* on Plates of Green-Bean Agar

sulfuric acid. In this way a constant relative humidity of approximately 95% was maintained throughout the experiment. The results of this experiment are graphically represented in Figure 3. It will be noted that the optimum temperature for growth here is 22.5° C.
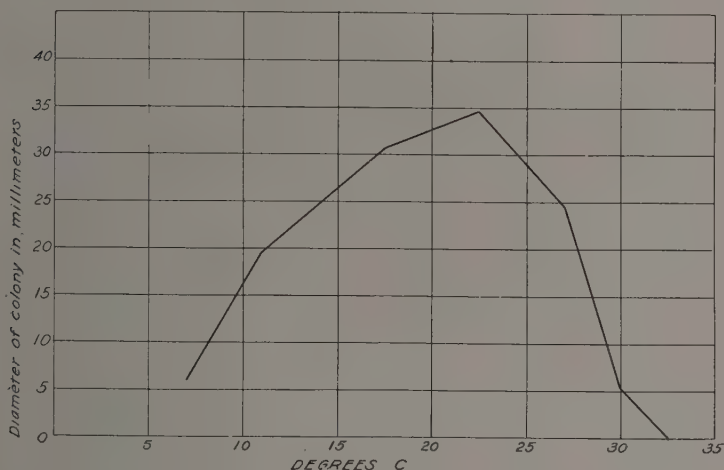

Fig. 3

Influence of Temperature on Growth of *Colletotrichum lindemuthianum* on Plates of Green-Bean Agar
All cultures were held at a constant relative humidity of approximately 95 per cent.

EFFECT OF THE MEDIUM

The cultural characters of micro-organisms on differential media have been used by various workers to distinguish between species or forms which could not readily be differentiated on a morphological basis. Appel and Wollenwebber (2) and Sherbakoff (40) have demonstrated clearly the value of this method of identification for species of Fusaria. Thom (47) also has been able to distinguish morphologically similar species by cultural characteristics on different media. The use of differential media is universal in bacteriology. It seems reasonable, therefore, to suppose that if sufficiently uniform conditions could be maintained, the biologic forms of *C. lindemuthianum* might be distinguished by their reactions on various media. All attempts, however, to do this with the usual nutrient agars have been unsuccessful. Several of the biologic forms have been grown side by side on several different agars in test tubes and petri dishes with this purpose in view. In several instances apparent differences were observed, but in as many cases there were greater differences in duplicate cultures of the same biologic form on the same medium. (Plate IV.) Nor could any constant differences be detected in the

character of growth of the various forms on sterilized bean pods. Careful and long-continued observations have shown that slight changes in moisture content of a medium often will cause much greater differences in growth characters in the same biologic form than have been observed between any of the different forms on any of the agars used. For example, three tubes of freshly prepared green-bean agar were inoculated with Culture 15, and five days later the culture was sporulating profusely. Seven days after the first inoculation other tubes of the same lot were inoculated with spores from the same original culture, but a very different type of growth was produced with no sporulation whatever.

It might be argued that this change in growth characters was due to a loss of the ability to sporulate. Such variations have been reported by Dastur (19) for certain species of Glomerella. That this was not the case is indicated by the fact that abundant sporulation occurred when the culture was transferred to sterilized bean pods.

Since Pasteur, in 1861, first demonstrated the specific action of *Penicillium glaucum* toward the dextro- and levo-tartaric acids, numerous cases of specific relationships between micro-organisms and carbohydrates containing assymetric carbon atoms have been reported (21, 24). A specific reaction toward the common sugars constitutes an important means of identification of bacteria (28). To find whether or not biologic forms of *C. lindemuthianum* differed in their action on such compounds, three biologic forms were cultured on a modified Czapek's solution in which the sucrose was replaced by 0.8 per cent of a given sugar or related compound. The carbohydrates used were purified biological products prepared by the Speciality Chemical Company, Highland Park, Ill. These were dissolved in water and sterilized by filtration through Mandler filters. Then the required amount was added by means of sterile pipettes to previously sterilized flasks of Czapek's solution from which the sucrose had been omitted. Duplicate 200-cc. flasks, containing 50 cc. of the solutions prepared in this manner, were inoculated with fresh spores and incubated at from 20° to 25° C. for two months. At the end of this period the dry weight of the mycelium produced by each biologic form on the various media, was determined. Table VI shows the results of the experiment.

Altho some growth was made by all three biologic forms on all the carbohydrates used, there was a remarkable difference in the amount of growth of the different biologic forms on certain of the solutions. The differences were especially marked on xylose and mannitol, where the amounts of mycelium produced by Cultures 5 and 6 were

approximately twice that produced by Culture 15. There was also a decided difference in the type of growth produced by the two forms on these solutions (Plate V).

TABLE VI

GROWTH OF THREE BIOLOGIC FORMS OF *Colletotrichum lindemuthianum* ON DIFFERENT CARBOHYDRATES

Carbohydrate	Dry weight of mycelium in mg.		
	Culture 5	Culture 6	Culture 15
Mannose	126	132	100
Maltose	76	66	66
Raffinose	116	88	92
Rhamnose	78	54	50
Xylose	52	56	28
Levulose	120	104	122
Mannitol	96	122	50

EFFECT OF THE CONCENTRATION OF HYDROGEN IONS IN THE MEDIUM

It has been demonstrated in numerous cases that micro-organisms react strongly to very slight changes in the concentration of hydrogen ions in the culture medium (52). Furthermore, the reaction of different organisms to different hydrogen-ion concentrations shows great variation. *C. lindemuthianum,* according to Edgerton (25), is very sensitive to acids and grows best in an alkaline medium. Edgerton's tests were made on agar titrated to various degrees of acidity and alkalinity as indicated by Fuller's scale. Since the reliability of Fuller's scale as an index of the true acidity of a medium is somewhat questionable (52, 15), it was thought desirable to repeat these tests, using the concentration of hydrogen ions as a criterion. Since the fungus grew readily on Czapek's solution,[2] this medium was chosen for the work. A series of solutions of different pH value was made up by adding to Czapek's solution various amounts of N/5 HCl and N/20 KOH, following approximately the curve given for this medium by Karrer and Webb (32). The pH value of each member of the series was first tested colorimetrically by the method given by Clark (16) and determined more accurately on a potentiometer just

[2] This solution contains 0.5 gm. magnesium sulphate, 1 gm. monobasic potassium phosphate, 0.5 gm. potassium chloride, 0.01 gm. ferrous sulphate, 2 gms. sodium nitrate, and 30 gms. cane sugar in one liter of distilled water.

before being inoculated. The cultures were made in triplicate on 50 cc. of the medium in 150 cc. Erlenmeyer flasks. A comparative test was made of two biologic forms, Cultures 5 and 15. The cultures were incubated at from 20° to 25° C. At the end of two months the dry weight of the mycelium produced was determined. The results are summarized in Table VII and are illustrated graphically in Figures 4 and 5.

TABLE VII

Growth of *Colletotrichum lindemuthianum* on Czapek's Solution at Various pH Values

Culture 5			Culture 15		
pH of medium		Dry wt. cf mycelium in mg.	pH of medium		Dry wt. of mycelium in mg.
Original	Final*		Original	Final*	
1 2	1.2	0	1.2	1.2	0
1.5	1.4	0	1.5	1.4	0
1.9	2.0	0	1.9	2.0	0
2.0	2.2	0	2.0	2.2	0
2.9	3.0	0	2.9	3.0	0
3.5	6.6	67	3.5	6.6	58
5.2	6.8	86	5.2	7.0	54
5.6	7.3	87	5.6	7.5	65
6.9	7.8	88	6.9	7.8	85
7.5	8.0	96	7.5	8.0	95
8.6	8.4	88	8.6	8.6	71
9.3	8.8	83	9.3	8.8	88
10.6	9.0	98	10.6	9.0	103
11.2	9.4	48	11.2	9.4	91
11.8	9.8 +	26	11.8	9.8 +	60

*Determined by colorimetric method only

The fungus obviously grows best in an alkaline medium. No growth was made by either biological form in a medium with a greater concentration of hydrogen ions than pH 3.5, altho some growth occurred in the most alkaline medium used, pH 11.8. In a preliminary experiment, in which the mycelium produced was not weighed, a few small colonies were formed at pH 11.9 but none at pH 12.2. Not only did the fungus grow better in an alkaline medium, but where growth in an acid medium occurred, the acidity of the medium was decreased.
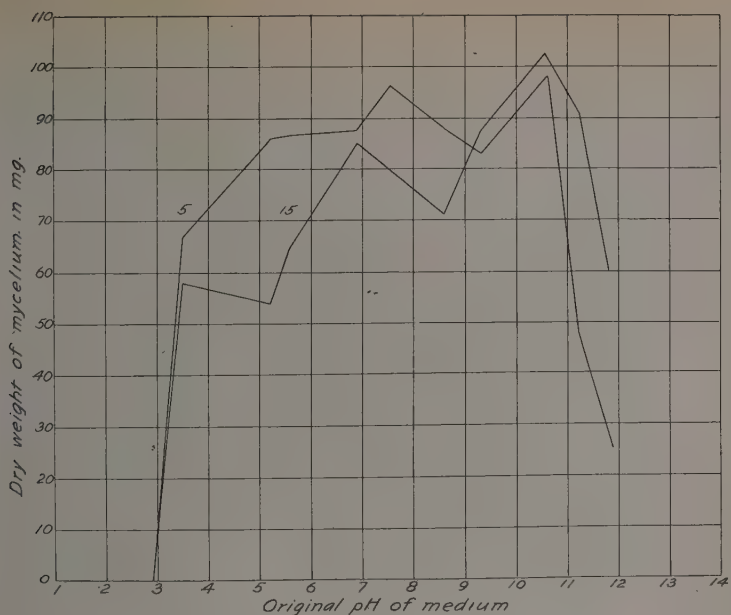
Fig. 4

Growth of Two Biologic Forms of *Colletotrichum lindemuthianum*, Cultures 5 and 15, on Czapek's Solution at Various Hydrogen-Ion Concentrations

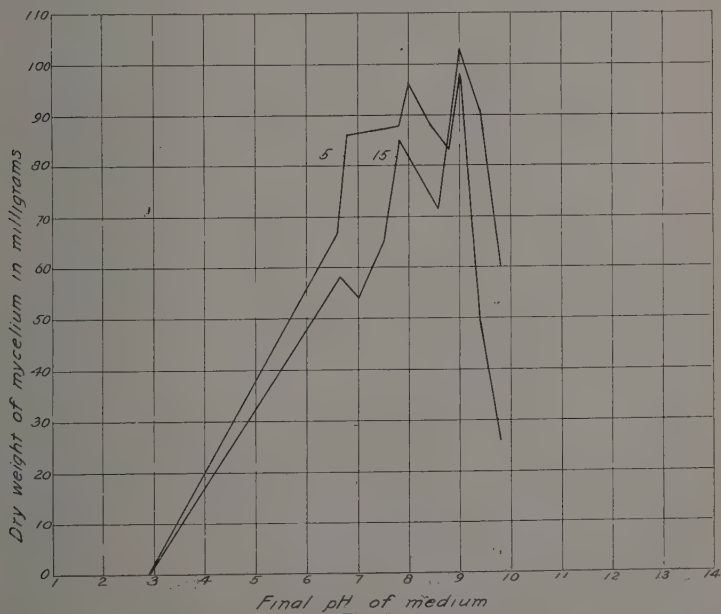Plotted on pH value of the medium at the time of inoculation.

Fig. 5

Growth of Two Biologic Forms of *Colletotrichum lindemuthianum*, Cultures 5 and 15, on Czapek's Solution at Various Hydrogen-Ion Concentrations

Plotted on the pH value of the medium after incubation for two months.

There was also a decrease in alkalinity of the more alkaline members of the series. This latter change was very probably due to the absorption of carbon dioxide from the air, as no precautions were taken to prevent this, and flasks of the solutions left uninoculated likewise became less alkaline.

The curves of growth of the two forms were, in general, similar. There appears to be a "double optimum" for both forms, but in one case it did not occur at exactly the same point for both forms.

PLASTICITY OF THE BIOLOGIC FORMS

It is important practically as well as interesting scientifically to know whether the parasitic capabilities of these biologic forms are stable and constant or whether they are plastic and variable. Eriksson (29) is of the opinion that the parasitic capabilities of biologic forms of *Puccinia graminis* are more or less modified by association with various hosts as well as by environmental conditions. Ward (49, 51) also thought that he was able to change the parasitic capabilities of the biologic forms of the brome rusts (*P. dispersa*) by growing them for some time on the proper host. It has been conclusively proved, however, by Stakman, et al, (44, 45) that the biologic forms of *Puccinia graminis* are relatively constant and are not easily modified. But since *C. lindemuthianum* is a facultative saprophyte it would be only reasonable to suppose that it might more readily be modified than a strictly obligate parasite. Experiments were made, therefore, to determine whether the parasitic capabilities of the biologic forms of *C. lindemuthianum* could be readily modified.

There are two ways by which, theoretically, such a change might be brought about: (1) by consecutive transfer of the pathogene from a susceptible variety to an increasingly resistant one, i. e., the use of the so-called "bridging hosts"; (2) by growing the fungus for several consecutive generations on a resistant host.

The conception of bridging hosts was first introduced by Marshall Ward (51). He concluded from inoculation experiments that a biologic form of *P. dispersa* which would not attack a given species of Bromus when transferred directly to it from another given species, could be made to do so if it was first transferred to a third one, intermediate taxonomically between the other two. The material used in this investigation offers nothing strictly analogous to the above. A problem, however, which is fundamentally similar exists. Thus Variety 20 is highly resistant to Culture 5 and very susceptible to Culture 15, while Variety 21 is very susceptible to Culture 5 and highly resistant to Culture 15. Variety 43 is very susceptible both to Culture

5 and to Culture 15, and theoretically might serve as a bridging host for either of these biologic forms. Numerous attempts were made to infect resistant varieties by first transferring the fungus to such theoretical bridging hosts. Several combinations of varieties were used, but all efforts were unsuccessful. The virulence of the parasite never was increased as a result of its development on such hosts.

In testing the second method, since the fungus is known to live over in the seed, it was realized that to avoid chances of error it would be necessary to have absolutely clean seed. For this experiment a variety (Pink), the seed of which was obtained from California,[3] was used. In order to avoid other chances of error the experiment was made in a greenhouse in which no other beans were grown. The procedure was as follows: The plants were inoculated and incubated in the usual manner. When numerous small to medium brown lesions had appeared, a stem was cut into sections about one-half inch in length. These were immersed for from three to five minutes in a mercuric bichloride solution (1-1000), then removed and washed in sterile distilled water and plated in agar. After about 48 hours the fungus had begun to grow throughout the tissue of most of the segments of bean stem, which were soon covered with spores. A distilled water suspension of these spores was made and used for inoculating another set of plants. This process was repeated for six generations without the slightest increase in the virulence of the pathogene. This experiment indicates that a biologic form of *C. lindemuthianum* does not increase in virulence by constant association with a resistant host.

CONSTANCY OF HOST RESISTANCE

Since all efforts to increase the virulence of the fungus failed, attempts were made to break down the resistance of the host. Salmon (39) reports experiments in which the resistance of certain species of Bromus to *Erysiphe graminis* was broken down by injuring mechanically the surface layers of the plant tissue. Stakman (41) was unable to break down the resistance of various hosts to *Puccinia graminis.*

Since *C. lindemuthianum* is a facultative saprophyte. it seemed possible that injury of the host tissue might predispose the plant or certain tissues to infection. It also seemed possible that an abundance of nutrients in the inoculation drop might give the fungus added infective power. A few experiments were made to determine whether the resistance could be overcome in this way. The results are given in Table VIII. These experiments were sufficient to convince one that

[3] This seed was very kindly furnished by Dr. J. T. Barrett.

such treatment would not overcome the resistance of a host plant.
Subsequent histological studies corroborated this fact.

TABLE VIII
RESULTS OF EFFORTS TO BREAK DOWN HOST RESISTANCE

H st Acc. No.	Variety	Previous reaction*	Treatment	Result
25	Black and White, Minn. Selection 1099	R	Spores sprayed on in Czapek's solution	No appreciable increase in virulence
26	Yellow Indian, Minn. Selection 1100	R		
33	Shoe Smith, Minn. Selection 73	R		
34	Small White, Minn. Selection 27	R		
39	California Wonder, Minn. Selection 43	R		
40	Black Turtle Soup, Minn. Selection 104c	R		
43	Long Yellow, Minn. Selection 142	S		
44	Newport Navy, Minn. Selection 1084	R		
37	Navy, Minn. Selection 59	R	Numerous pin pricks over surface of stems	R. Some browning around pricks but no typical lesions —no fructification
38	White Wonder, Minn. Selection 26c	R		
37 ·	Navy, Minn. Selection 59	·	Checks not inoculated	Tissue around pricks slightly browned.
38	White Wonder, Minn. Selection 26c	R	Checks not incoluated	Tissue around pricks slightly browned
42	Navy, Minn. Selection 1088	R	Stems split lengthwise	R. Browning of exposed tissue—no lesions
42	Navy, Minn Selection 1088	R		Check similar to above
79	Arikora	R	Epidermis scraped off one side of stem	R. Lesions slightly larger where epidermis was removed but no normal infection.
81	Red Mexican	R		

*Culture No. 2 was used throughout the experiment.

SPORE GERMINATION

The process of spore germination in *C. lindemuthianum* has been
described by Atkinson (3), Edgerton (25), Dey (20), Barrus (7),
and others. It is not necessary, therefore, to describe the process at
length. Under the most favorable conditions spores may germinate
within 8 or 9 hours, but they usually require somewhat longer; and
some may not germinate for days, altho, to all appearances, conditions

are favorable. One or more germ tubes (seldom more than two) are sent out from any portion of the spore, altho they arise most commonly from the side and near the end. The size and length of the germ tubes differ on different media. In nutrient media the germ tubes commonly grow directly into profusely branching mycelium, altho appressoria may be formed. In non-nutrient solutions appressoria are formed if the germ tube comes into contact with a hard surface; otherwise the germ tube distintegrates without further development. The appressoria are apparently thick walled and dark brown in color. The shape is more or less spherical and the diameter is from 6 to 10 microns. The spores may or may not become septate on germination. Under unfavorable conditions germination may be abnormal.

All the writers mentioned above commented on the difficulty of securing a high percentage of germination, especially in distilled or tap water. Webb (52) was forced to discard *C. lindemuthianum* from the fungi selected for study of spore germination as affected by hydrogen-ion concentration, because of his inability to secure germination in control solutions. Edgerton (25) and Barrus (7) state that the spores germinate better in nutritive solutions than in distilled or tap water.

In the first spore germination experiments made by the writer, spores were taken from a sterilized bean pod and placed in hanging drops of distilled water. Less than 2 per cent of the spores germinated. It was observed that in placing the spores in the hanging drops of water some of the gelatinous matrix surrounding the spores also was introduced. This substance readily dissolves in the water. Since spores never germinate while still imbedded in this matrix, it was thought that some inhibiting substance might be carried over into the hanging drop. If this were true, the substance should be removed if the spores were washed sufficiently. Therefore, a dense spore suspension was made in 15 cc. of distilled water, placed in a centrifuge which was run for 2 minutes at 1800 revolutions per minute. The liquid was then poured off. A quantity of spores were then transferred from the bottom of the centrifuge tube to hanging drops of distilled water. Distilled water was again added to the spores in the centrifuge tube. The spores were thoroly agitated and centrifuged for two minutes as before. This process was repeated five times, a mount of spores being made after each washing. For the results of the germination tests see Table IX. It will be observed that washing did not appreciably increase germination, altho a lower percentage of the unwashed spores germinated. Apparently the matrix is not responsible for the poor germination in distilled water. If there is

an inhibiting substance in the matrix its action must be specific because it did not inhibit the germination of spores of *Fusarium lini* when they were sown in the liquid decanted after the first washing.

TABLE IX

EFFECT OF WASHING ON SPORE GERMINATION

Treatment of spores	Solution	Per cent germination
Not washed	Distilled water	± 1
Washed once	Distilled water	2-3
Washed twice	Distilled water	2-3
Washed three times	Distilled water	2-3
Washed four times	Distilled water	2-3
Washed five times	Distilled water	2-3
Washed five times	Liquid decanted after first washing	2-3
Fusarium lini	Liquid decanted after first washing	95-100
Fusarium lini	Distilled water	95-100

In an effort to secure a medium in which a uniformly high percentage of germination could be obtained, many germination tests were made with various media and under various conditions. Too much space would be required to give these in full. A few of the essential and representative ones are presented in Table X.

TABLE X

EFFECT OF VARIOUS MEDIA ON SPORE GERMINATION

Medium	Per cent germination*
Distilled water	6
Tap water	8
Czapek's solution	11
Czapek's solution, 1 part, bean decoction, 1 part	10
Bean decoction	8
Bean decoction, 1 part, distilled water, 1 part	5
Pean decoction, 1 part, distilled water, 5 parts	7
Distilled water plus a small piece of fresh bean tissue	83
Green-bean agar	97
Potato dextrose agar	98

*An average of three or more separate tests replicated not less than three times in each test.

A number of interesting facts were discovered in these tests. The addition of a small bit of leaf tissue stimulates spore germination to a remarkable degree. In a number of the tests positive chemotropism of the germ tubes was induced by the leaf tissue. (Fig. 6). This is not always evident, owing, probably, to a more rapid diffusion of the stimulating substance throughout the drop. In a few of the tests

fresh tissue did not stimulate germination. These cases, however, were rare. Boiled bean decoction did not stimulate germination. Fresh bean juice, on the other hand, was as effective as the piece of tissue. The synthetic nutrient solutions used did not stimulate germination. The fungus, however, will grow luxuriantly on Czapek's solution. The best germination was obtained when the spores were plated in nutrient agar.

Fig. 6

Camera Lucida Sketch of Germinating Spores of *Colletotrichum lindemuthianum* Manifesting Chemotropic Response Under the Stimulus of a Piece of Fresh Bean Tissue Less than one per cent of the checks in distilled water germinated.

In order to learn more about the nature of the stimulating substance found in fresh bean tissue, a series of germination tests was made in distilled water in which the effects of fresh tissue of various plants were compared. Tissues from resistant and susceptible bean varieties also were compared. The results, summarized in Table XI, indicate that sunflower, corn, and wheat tissue can stimulate spore germination but not so much as bean tissue does. Tissues from resistant and susceptible bean varieties apparently stimulate germination equally well. In one test in which spores of two biologic forms were germinated in contact with tissue of one variety, there were indications of a difference, but subsequent tests showed that this particular lot of spores would not germinate even in contact with tissue of a susceptible variety. This difference in germination of different lots of spores of the same age under apparently identical conditions has been observed on several occasions. The writer can offer no explanation of the phenomenon.

TABLE XI

Effect of Fresh Tissue of Various Plants on Spore Germination

Medium	Per cent germination		Remarks
	24 hrs.	40 hrs.	
Distilled water	± 1	3	
Distilled water plus tissue of resistant bean	±95	±95	Normal germination
Distilled water plus tissue of susceptible bean	±95	±95	Normal germination
Distilled water plus sunflower tissue	± 1	5	Considerable abnormal budding
Distilled water plus wheat tissue	± 1	12	Considerable abnormal budding
Distilled water plus corn tissue	± 1	10	Considerable abnormal budding
Distilled water plus tomato tissue	± 1	2	Considerable abnormal budding
Czapek's solution	± 1	5	Considerable abnormal budding
Czapek's solution plus susceptible bean tissue	±95	±95	Normal germination
Czapek's solution plus resistant bean tissue	±95	±95	Normal germination

The fact that boiled bean decoction failed, while fresh bean extract succeeded, in stimulating germination to a marked degree, would indicate that the stimulating substance was destroyed by heat; yet it should be remembered that very good germination was obtained in green-bean agar made from a similar decoction. A fairly high percentage of germination has been obtained also in non-nutrient agar. It is possible that two distinct stimulating factors are involved.

Brown (11) has observed that Botrytis spores germinate readily in "infection drops" on the surface of host tissue, while they germinate very poorly in distilled water. He has demonstrated that the stimulation is due to substances passing into the "infection drop" by exosmosis from the host tissue. The stimulation has been correlated with a high conductivity of the solution in the infection drop. The spores, however, do not germinate in tap water which has a relatively high conductivity.

Such exosmosis of stimulating substances into the infection drop may play an important part in infection by *C. lindemuthianum*. Heavy infection is easily obtained when a distilled water suspension of spores is atomized on to the plant. No extensive experiments along this line, however, have yet been made.

An attempt was made to determine the effect of the hydrogen-ion concentration of the medium on spore germination. The necessity of adding fresh bean tissue or juices to the medium in order to get a high percentage of germination made it difficult to obtain accurate results. Such procedure, of course, alters the pH value of the medium Czapek's solution minus the sugar was made up to various pH values with N/5 HCl and N/5 KOH. Spores were planted in hanging drops of these solutions. Fresh bean tissue was added to one series of mounts. In order to avoid bacterial contamination the tissue added was taken from plants grown from sterilized seeds in sterile test tubes and was handled under aseptic conditions. The results are summarized in Table XII. It will be observed that no germination occurred in a more acid medium than pH 3.4 with the exception of less than one per cent at pH 2.6 when the tissue was added. A trace of germination was obtained in a solution as alkaline as pH 9.6. The stimulating effect of the tissue was noticeable only between pH 3.4 and pH 7.

TABLE XII
Effect of Hydrogen Ions on Spore Germination

pH	Per cent germination		pH	Per cent germination	
	No tissue added	Tissue added		No tissue added	Tissue added
1.2	0	0	5.8	5	93
1.5	0	0	6.0	± 1	78
2.0	0	0	6.5	± 1	58
2.6	0	1	7.0	± 1	11
3.4	1	76	8.0	3	± 1
4.6	1	75	9.6	± 1	± 1
4.8	1-2	73	9.6+	0	± 1
5.0	4	92	Dist. H²0	2	90

Germination tests to determine the effect of temperature were made by plating the spores in green-bean agar and incubating at various temperatures. The results are given in Table XIII. It is interesting to note that germination takes place more rapidly at temperatures higher than the optimum for growth but that germ tubes do not develop normally at 27.5° C. or higher. The critical temperature evidently lies somewhere between 32° and 35° C.

TABLE XIII

Effect of Temperature on Spore Germination

Temperature Degrees C	Per cent germination*			Remarks
	20 hrs.	40 hrs.	100 hrs.	
5	0	0	2	Germinated 95 per cent when changed to 17°.
12	7	8	51	Bud-like secondary spores formed.
17	18	51	85	Normal germination for most part, but numerous bud-like secondary spores also present.
22	40	47	92	Normal germination.
27.5	46	96	96	Normal germination at first but later becoming abnormal.
32	71	97	97	Abnormal germ tubes; short and twisted.
35	0	0	0	
37	0	0	0	

*An average of several tests.

INFECTION AND DEVELOPMENT OF THE FUNGUS IN THE HOST

Dey (20) has carefully worked out and described the mechanism of penetration of *C. lindemuthianum* into a susceptible host. Further development of the fungus was not studied. Nor was the process of penetration into a resistant host observed. Edgerton (25) and Barrus (7) each have described in more or less detail the development of the fungus within the tissue of a susceptible host.

Dey (l.c.) concluded that both the spore and the appressorium became attached to the cuticle, the latter by means of a mucilaginous sheath. No such sheath was observed around the spore. This fastened the germ tube at both ends, so that its further growth caused it to curve up, thereby exerting pressure sufficient to cause a slight indentation of the epidermal cell wall. On the under side of the appressorium a slight protuberance was then formed which pushed in the cuticle still farther. From this protuberance a very fine infection hypha developed which ruptured the cuticle. No dissolution of the cuticle was observed, indicating that the process was purely mechanical. After passing through the cuticle the infection hypha gradually enlarged, at the same time causing a dissolution of the cellulose layers. After growing a short distance into the cell the infection hypha formed a vesicle from which one or more branches emerged. These

observations were made on stained sections of pods from material imbedded in paraffin.

The writer has endeavored to trace the development of the fungus in both susceptible and resistant varieties. Observations were made on both fresh and imbedded material. Infection was first observed by examining strips of the epidermis, peeled from bean stems which had been previously inoculated and incubated in the usual manner. The further development was observed in imbedded material and in fresh sections cut on a freezing microtome or on a sliding microtome. The imbedded material was killed at various intervals in medium chromacetic, picric acid (sat. sol. in 70 per cent alcohol) or formalin alcohol. This material was imbedded in paraffin in the usual manner, cut in sections ranging from 3 to 13 microns in thickness, and stained with light green and diamant fuchsin. A splendid contrast was obtained with this combination of stains. The cuticle, lignified tissue, and host nuceli, as well as the fungous mycelium were stained a deep purplish red, while the cellulose tissues were stained a bright green. The host protoplast also stained red, but it was not sufficiently dense to decrease, to any appreciable extent, the contrast between mycelium and cell wall.

It was found that penetration is accomplished in the same manner and equally well on susceptible and resistant varieties. The writer did not observe the attachment of the spores to the epidermis as reported by Dey (20). Nor did he observe any upward bending of the germ tube due to growth after the appressorium and spore had become fastened. As a matter of fact, in a large majority of the cases observed the germ tube was extremely short and apparently did not increase in length after the appressorium was formed. (Plate VI, Figs. 1, 2, and 9). In rare instances a well developed germ tube was observed but in such cases the spore was easily displaced. The appressorium, however, was very firmly attached by a gelatinous matrix. (Plate VI, Figs. 2, 4, and 10. Plate VIII, Figs. 2 and 5.) The actual penetration of the cuticle by the infection hyphae could not be seen with sufficient detail to judge whether or not it was accomplished by mechanical pressure. This is very probably the case, as no solvent action could be detected; and since the appressorium is fastened to the epidermis, it is reasonable to suppose that sufficient pressure could be developed to effect an entrance in this way. The infection hypha at the point of penetration is without doubt extremely small.

DEVELOPMENT OF THE FUNGUS IN A SUSCEPTIBLE HOST

After penetration of the epidermal cell wall of young susceptible tissue, the infection hypha rapidly enlarges, often filling the entire

epidermal cell as seen in cross-section. (Plate VI, Figs. 2 and 4. Plate VII, Fig. 4.) Further development shows that this enlargement is not of the nature of a vesicle, as assumed by Dey (20). It is, on the other hand, merely thickened mycelium, due partly to an abundant food supply and partly to retardation of apical growth, caused by the resistance of the cell wall to penetration. If a thin cross-section is cut from an infected stem about four days after inoculation, the nature of the early stages of development can readily be observed. Practically all of the mycelium which develops during the first 48 hours after penetration is of this thickened type, and for the most part adheres closely to the cell wall for approximately one-half of its inner circumference. (Plate VI, Figs. 2 and 4. Plate VII, Figs. 1, 2, and 3.) In the rare cases in which the mycelium does extend directly across the cell cavity a still greater enlargement occurs at the point of cell-wall penetration. (Plate VI, Fig. 5. Plate VII, Fig. 1.) This does not agree with the ideas of Barrus (7), who illustrates small strands of mycelium uniform in size, radiating from a point near the epidermis and passing directly across the cell cavities. Since this mycelium differs greatly from that which is developed later, the term "primary mycelium" has been applied to distinguish it from the latter which will be called the "secondary mycelium."

In the penetration by the primary mycelium only a very small hole is made in the cell wall. The hole is usually less than one tenth the diameter of the mycelium. (Plate VI, Figs. 2 and 5).

Approximately fifty hours after penetration the primary mycelium has made its way through the cortex, involving a relatively small number of cells and with very little effect on their structure. At about this time, however, many smaller hyphae develop and spread rapidly in all directions. The tissues of the bean stem at this time have a decidedly water soaked appearance around the point of infection, indicating that the intercellular spaces have become filled with liquid. This secondary mycelium commonly passes directly across the cells and penetrates the cell wall with little or no permanent enlargement or bending. (Plate VI, Figs. 6, 7, and 8. Plate VII, Fig. 5.) A much larger hole is made in the cell wall and there is very little constriction in the mycelium at the point of penetration. Of course all gradations between the two types of penetration occur, but the change in type is rapid and complete. The secondary mycelium penetrates the tissue in all directions but in the stems and leaf petioles it advances more rapidly upward and downward. This is due to the fact that the cells of the cortex are much longer in this direction and the mycelium has fewer cell walls to penetrate.

It is quite evident that the differences in character of the primary and secondary mycelium are due to the difference in resistance offered by the cell walls. It has not been possible to determine conclusively the exact means by which cell-wall penetration is accomplished. The mechanical pressure of the growing mycelium undoubtedly is an important factor. (Plate VI, Fig. 3. Plate VII, Fig. 3.) This is especially true of the primary mycelium as indicated by the thickening and bending of the hyphae. The peculiar adherence of the primary mycelium to the cell wall (Plate VI, Figs. 2, 3, and 4. Plate VII, Figs. 1 and 2.) plainly is due to bending of the hypha after the apex has reached the opposite side of the cell.

In the later stages, however, the cell walls have in some way become softened. In sections of material fixed 126 hours after inoculation, small thread-like mycelium can be seen penetrating the cell walls as if they were extremely soft and gelatinous. (Plate VI, Figs. 6, 7, and 8. Plate VII, Fig. 5.) The immediate cause of the softening of the cell walls has not been determined. The fungus very probably secretes an enzyme or some other substance which might have such an effect but as yet no efforts have been made to identify it. If the softening is due to the secretions of the fungus the substance diffuses very rapidly, for there is no localization of the softening effect in the immediate vicinity of a mycelial strand. It is also possible that a certain amount of autolysis might take place after an initial number of host cells are attacked by the fungus. Such substances, if set free on the penetration of the cell by the fungus, would spread rapidly with the sap which, obviously, flows into the intercellular spaces as has been previously described. Cases have been observed in which the middle lamella quite clearly has been dissolved, but this occurs chiefly in the later stages of development and is by no means general.

The growth of the mycelium within the tissues was observed in sections of the living material, made at various intervals after inoculation. The progress of a mycelial strand through two cell walls is illustrated in Plate VI, Fig. 3. The section from which this sketch was drawn was cut free hand 72 hours after inoculation. At the time the section was cut the thickened primary mycelium was abundant, but there was very little mycelium of the secondary type. The section was mounted in water, left for three hours, and examined again. Small strands of mycelium had begun to grow in all directions through the tissue and out into the water. When the mycelial strand which is illustrated here was first observed, it had not yet reached the point of penetration *a*. It reached *a* at 8:09 o'clock. At 8:30 penetration at *a* was complete. In the meantime the mycelium had slowly bent over to the cell wall at the side where it remained. There was a

slight swelling at the tip, most of which disappeared as soon as penetration had occurred. The distance from *a* to *b* was 55 microns. At 9:29 *b* was reached. This time the mycelium did not bend to one side but became slightly wavy. As soon as penetration was accomplished (9:47) it again became straight. Here the two cell walls were pulled apart for some distance before the second one was penetrated at *c* (10:04). The observation of such phenomena convinces one that mechanical pressure is indeed a very important factor in cell-wall penetration by the fungus. The process here outlined resembles very much that described by Hawkins and Harvey (31) for *Pythium deBaryanum* on the potato tuber. The rate of growth, however, was only about one-tenth that of *P. deBaryanum;* and the time required for penetration of a cell wall in the cases observed was approximately twenty minutes, or about four times as great. There is apparently another difference in the greater increase in diameter of the mycelium of *C. lindemuthianum* and the permanence of this character, as well as that of the bending of the mycelium. Moreover, no softening of the cellulose layers of the cell walls was observed in the potato tubers, while in the bean such softening is very pronounced in the later stages of development.

There is very little discoloration of the tissue of a susceptible host during the early stages of infection. Cell after cell may be almost completely filled with the large primary mycelium, and yet show no discoloration. And, moreover, the host protoplasm does not seem to be injured appreciably. At least there is no apparent disorganization or disintegration. Sometimes the fungus almost filled the cell cavities with large, thick primary mycelium which apparently developed between the protoplasmic membrane and cell wall, crowding the protoplast into a small compact mass against the cell wall. The organization of the protoplast, however, was not destroyed. (Plate VI, Fig. 4.) (The above applies, of course, only to young, susceptible tissue. The effect on tissue of a susceptible plant which has become resistant owing to age is quite different, as will be described later.) There is very little destruction of tissue until the secondary mycelium begins to develop, about 100 hours after penetration. When this happens there is a rapid collapse and discoloration of parasitized cells. About 125 hours after infection the mycelium has a tendency to grow toward the surface, and aggregations form just beneath the epidermis. The sporophores arise in palisade layers from these, rupture the epidermis, and produce a slimy mass of spores.

In old tissue the primary mycelium advances much more slowly, the rate depending upon the age of the tissue. If the tissue is sufficiently old, only a very few cells are penetrated. If the fungus has not advanced more than three or four cells beneath the epidermis,

about 72 hours after inoculation discoloration is very pronounced and the mycelium shows signs of disintegration. Later the parasitized cells are completely killed and then they collapse. The mycelium also distintegrates without the production of secondary mycelium or spores. All gradations between the two conditions occur, depending upon the age of the tissues. It is hardly to be doubted that the failure of the mycelium to develop is due to the increased resistance of the cell wall to penetration. Whether it is due to resistance to mechanical penetration, or to an increased resistance to an enzyme secreted by the fungus can not be stated with certainty. The former undoubtedly is very important. More extensive biochemical studies would probably throw some light on the subject.

The characteristic lesions produced by *C. lindemuthianum* on a susceptible host are typical of what is termed local necrosis. The dependence of the fungus on mechanical pressure for its advance through the tissue and the increased resistance of the tissue as it becomes older, very probably explain the cause of the local necrosis. Thus, a young, rapidly growing bean pod is infected, but before the fungus has had time to develop extensively the tissue has become suf- ficiently old to check its further advance. That the extent of the necrosis depends largely on the age of the tissue is well illustrated in Plate 1, Figures 2 and 3. Some varieties of beans undoubtedly develop such resistance much earlier than others, and it is very prob- able that some varieties that are resistant to all the biologic forms owe their resistance to this fact.

DEVELOPMENT OF THE FUNGUS IN A RESISTANT HOST

When a highly resistant host such as Variety 21 (Ruby Horticul- tural Bush, Minn. Selection 3B-18) is inoculated with Culture 15, rarely more than one or two cells are attacked. The infection hypha seems to meet an unfavorable environment as soon as it has penetrated the outer epidermal cell wall. Sometimes the mycelium may be checked before it reaches the opposite wall of the epidermal cell (Plate VIII, Fig. 5) ; again it may succeed in penetrating this wall, but it seldom advances farther. (Plate VIII, Figs. 1 and 4. Plate VI, Fig. 10.) As soon as the mycelium has been checked the cell walls and protoplast are stained reddish brown. Cell walls so discolored lose their affinity for light green and take up the diamant fuchsin instead. (Plate VI, Figs. 10 and 11. Plate VIII, Figs. 2, 3, and 5.) These cells soon collapse completely. The mycelium and host protoplast both disinte- grate and stain a homogeneous deep red with diamant fuchsin. (Plate VI, Figs. 9, 10, and 11. Plate VIII, Figs. 2, 3, 4. 5, and 6.) The host protoplast in this case seems to be extremely sensitive to the invading mycelium, while in a susceptible host the mycelium apparently

passes through without any immediately detrimental effects. (Plate VI, Fig. 4.) In the tissues of less resistant varieties the fungus may advance through a considerable number of cells but the end result is the same.

The retarding of the fungus here undoubtedly is due to some quality of the protoplast and not to the resistance of the cell walls, altho the final result and the discoloration phenomena are somewhat similar to those which occur in the older tissues of susceptible varieties. The resistance here also is specific, for this same variety is completely susceptible to Culture 5. (Plate II, Fig. 1.) Here then we have two types of resistance, each due to a different factor; in one case a non-specific factor, i.e., age of tissue, and in the other a specific factor lying within the protoplast. A recognition of this fact should be of some significance in the breeding of beans for resistance to anthracnose, since in all probability it would be much easier to deal with a single non-specific factor controlling resistance to all biologic forms of the fungus than with a specific factor for each one. Barrus (6) has discovered one variety of merit (Wells' Red Kidney) which seems to be resistant to all the known biologic forms of the fungus and Burkholder (12) has succeeded, by crossing, in uniting the resistance of this variety with the desired characteristics of the White Marrow. It would be interesting to know which factor controls resistance in this case.

The sequence of results described above, namely, cell penetration and absorption of food without immediate death and disorganization of host protoplast, in susceptible tissues, and the death and disintegration of both the invading mycelium and a limited number of cells in resistant tissues, is strikingly similar to that described by Marryat (36) for *Puccinia glumarum* on two immune varieties of wheat and by Stakman (42) for *Puccinia graminis* on hosts highly resistant to its attack. This similarity suggests the possibility of an explanation similar to that offered by Marryat (l.c.) for the death and disintegration of the invading mycelium, namely, starvation. But *C. lindemuthianum* is a facultative saprophyte and should be able to utilize the food products set free by the dead host cells. This in all probability would be the case provided the host cells were killed before the death of the mycelium. We have no proof, however, that such is the case. In fact all visual evidence tends to indicate that the fungous mycelium disintegrates first and that it is the products of such disintegration that kill the host cells and stain the cell walls. Intact mycelium never has been found in a collapsed cell of a resistant host.

Of interest in this connection is the work of Dox and Maynard (22) in which it was shown that when molds were grown upon a fluid synthetic medium the nitrogen was almost completely taken up by the

mycelium during the vegetative period and then gradually returned to the medium after growth had ceased. This was accompanied by a corresponding loss in weight of the mycelium. "During this time the mycelium lost its turgidity and the medium became *dark in color,* altho it retained its original clarity. This phenomenon was ascribed to the autolysis of the fungus."[4] Further work along this line by Dox (23) showed conclusively that the autolysis was due to the exhaustion of the carbohydrate from the medium.

All the evidence obtained from the writer's histological studies indicates that the mycelium on entering the cell of a resistant host is unable to get sufficient food for its nourishment and promptly undergoes autolysis, and that the products of this autolysis are fatal to the host cell. If this is true it would seem that there must be some specific difference in the nature of the food materials elaborated in the cells of a resistant plant from those elaborated in the cells of a susceptible plant and a corresponding specificity of assimilation capabilities of the fungus.

Numerous cases of specificity of fungi in regard to assimilation have been reported. The classic work of Pasteur who demonstrated the relation of *Penicillium glaucum* to the isomeric tartaric acids has been referred to in a previous paper by the writer (34) and is too well known to be repeated here. Dox and Roark (24) have shown a striking difference in the rate of utilization of alpha- and beta-methyl glucoside by *Aspergillus niger.* The fungus grows readily on the beta-form but makes extremely scant growth on the alpha-form. Furthermore the writer has presented evidence, in this paper, of a difference in ability of the biologic forms of *C. lindemuthianum* to assimilate certain carbohydrates.

An effort was made to determine whether there was a specific food substance in the resistant host which could not be assimilated by the particular biologic form of the parasite. The sap was expressed with a screw press from about 200 seedlings of Variety 21, which is highly resistant to Culture 15 and very susceptible to Culture 6. The plants were frozen prior to the extraction. The extracted sap was sterilized by filtration through Mandler filters. Duplicate flasks were inoculated with the above mentioned cultures. Both cultures grew equally well on the extract. This at first seems to indicate that no such specific food substance occurs in the resistant plant, but it does not necessarily do so. If, in the process of extraction, a substance capable of assimilation, not found in an available form in the living cell, is set free, the fungus would utilize it and leave the other just as *Penicillium glaucum* on racemic tartaric acid uses the dextro-form and leaves the levo-form. It is entirely possible that the food substances are held by the living

protoplasm in a particular state which is not available to a given biologic form of the fungus but is made available on the death of the protoplasm. This is a point, however, which is very difficult either to prove or disprove. The mechanism of nutrition and assimilation by protoplasm is a phenomenon about which we know very little and it probably will not be until we know more about this that the problem of disease resistance will be solved.

It should be pointed out that the parasitism of *C. lindemuthianum* as here described differs fundamentally from that of other non-obligate parasites which have been carefully studied. It has been assumed generally that parasitic fungi other than the strictly obligate parasites first killed the host cells, then obtained their nourishment from the products of the dead cells. The ability to obtain nourishment from living host cells has been attributed only to the obligate parasites. Brown (10, p. 125) expresses this conception as follows: "With highly specialized 'obligate parasites' the reactions between host and parasite are of a very recondite nature, and as yet there seems no possibility of subjecting them to experimental analysis. . . . In the case, however, of less specialized forms such as Botrytis, the reactions of host and parasite are comparatively simple in virtue of the phenomenon of 'action in advance.' On this account the host plant can be treated as a special kind of culture medium. Thus the problem entails simply the investigation of the growth of the parasite in a culture medium together with that of the enzymic process by which the living plant is converted into a dead culture medium." Such "action in advance" by means of which the living protoplasm is transformed into a dead culture medium has been demonstrated for Botrytis by Brown (9) and for *Pythium deBaryanum* by Hawkins and Harvey (31). The latter authors conclude from this that for the fungus in question "it seems hardly probable that resistance to fungus attack can be due to the living protoplasm."

C. lindemuthianum, however, does not normally kill the host cell in advance of its growth but, on the other hand, penetrates a large number of cells without any immediate lethal effect and quite obviously obtains nourishment from the living cells. All evidence seems to indicate that resistance is due to the inability of the fungus to obtain nourishment from the living protoplast.

SUMMARY

1. At least eight distinct biologic forms of *Colletotrichum lindemuthianum* were found as a result of comparative inoculations made with fifteen cultures of *C. lindemuthianum* on fourteen varieties of field beans.

2. The size of the lesions produced on a susceptible bean plant, when inoculated with *C lindemuthianum*, was inversely proportional to the age of the tissue inoculated; the older the tissue, the smaller the lesion. For this reason the age of the plant must be taken into consideration when interpreting the results of comparative inoculations. The age of the tissue had no effect on the size of the lesions produced on a highly resistant variety.

3. The size of the spores of *C. lindemuthianum* was influenced by the medium on which they were produced. Different biologic forms, however, were not influenced in the same way by the same medium. The variations in size due to the influence of the medium were sometimes as great as or greater than the difference in size of the spores of two forms on the same medium. Therefore the differences in size of spores of the biologic forms are not considered of any practical significance.

4. The cardinal temperatures for the growth of *C. lindemuthianum* on agar plates are approximately as follows: 0°C, 22.5°C, and 32°-34°C. The reaction to temperature, as indicated by rate of growth, was approximately the same for three biologic forms.

5. The common nutrient agars were not useful as differential media. In some cases there were apparent differences in growth of two biologic forms on the same agar but more often there were greater variations within replicate cultures of the same biologic form. Such variations were not permanent.

6. Some biologic forms of *C. lindemuthianum* grew better than others on certain modifications of Czapek's solution. This difference was the greatest when xylose or mannitol replaced the sucrose. The differences on these media were manifested by both the amount and the character of mycelium produced.

7. *C. lindemuthianum* grew best in an alkaline medium. No growth occurred on Czapek's solution more acid than pH 2.9. When growth occurred on an acid medium it was made alkaline. The fungus grew fairly well on Czapek's solution, as alkaline as pH 11.8 at the beginning of the experiment. Such solutions, however, were less alkaline two months after inoculation. This decrease in alkalinity was in all probability due to the absorption of carbon dioxide from the air. The growth of the two biologic forms tested was, in general, similar at the various pH values. There appeared to be a "double optimum," both optima falling on the alkaline side.

8. Efforts to change the parasitic capabilities of a biologic form of *C. lindemuthianum* were unsuccessful. Also all efforts to break down host-resistance failed.

9. Spores of *C. lindemuthianum* germinated poorly in distilled or tap water and in certain other solutions either with or without nutrients. Fresh bean tissue or fresh bean juice stimulated spore germination to a remarkable degree. Such tissue also often stimulated positive chemotropism of the germ tubes. The nature of the stimulating substance has not been determined. Good germination was obtained in green-bean agar.

10. The concentration of hydrogen ions in the medium was not the cause of the poor germination. The effect of various concentrations of hydrogen ions in the medium was not accurately determined on account of the necessity of adding tissue to induce normal germination. The stimulation of germination was obtained only between pH 3.4 and pH 7.

11. Spore germination occurred between $0°$ and $32°$C. Most rapid germination was obtained at the higher temperatures but at $27.5°$C., or above, the germination was abnormal from the first or shortly after. Bud-like secondary spores were formed at $17°$C. or lower.

12. Penetration of the epidermal cell wall is accomplished in the same manner and equally well on susceptible and resistant varieties of beans. The spore, when germinating on the host, forms an appressorium almost immediately, which becomes attached to the cuticle by means of a mucilaginous sheath. A small infection thread is sent into the epidermal cell, apparently by mechanical penetration.

13. In young tissue of a susceptible variety the infection hypha rapidly enlarges into a normal mycelium and continues its growth without bringing about the immediate destruction of the host protoplast. When the inner cell wall is reached, a resistance is met which retards apical growth, causing the mycelium to become greatly enlarged and often causes it to bend outward and become closely appressed to the cell wall for approximately one-half its circumference. Penetration finally takes place through a very small hole without any staining or swelling of the cell wall. This process is continued throughout numerous cortex cells until about 100 hours after penetration, when the cell walls seem to become softened throughout the region of infection. The mycelium then resumes its normal size and pushes its way through the cell walls with little or no constriction. At about this time the tissue begins to collapse and is usually stained brown. Strands of mycelium collect beneath the epidermis, produce acervuli, and rupture the epidermis with a mass of spores.

14. In old tissue of susceptible varieties, the mycelium is retarded in its development by increased resistance of the cell walls to penetration. Such retarded mycelium disintegrates, killing the host protoplast and staining the cell wall and its contents reddish brown.

15. Growth of the mycelium and cell-wall penetration was observed in freshly cut sections of living material. The fungus penetrates through numerous cells without killing the host protoplast. The bending and swelling of the hyphae during cell-wall penetration indicate that mechanical pressure is an important factor in the process, especially during the early stages of development.

16. In the early stages of normal infection of a susceptible host, *C. lindemuthianum* obtains its nourishment from the living host protoplast.

17. *C. lindemuthianum* will grow equally well on expressed juice of resistant and susceptible hosts.

18. In a highly resistant variety, seldom more than one or two cells are attacked. The fungus hyphae soon disintegrate and during this process bring about the death and disintegration of the host protoplast, at the same time staining the entire cell contents, as well as the cell walls, reddish brown. In a less resistant variety more cells may be attacked but the mycelium always disintegrates sooner or later with the same destruction and staining of the host protoplast. This process is interpreted as a nutrition phenomenon, the mycelium being destroyed by autolysis induced by starvation and the resulting products killing and staining the host cells. This is in keeping with what is known to take place when fungi are starved in artificial culture.

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PLATE I

Lesions Produced by *Colletotrichum lindemuthianum*

Fig. 1. Representative types of lesions produced on stems of bean seedlings in the greenhouse. See page 7 for explanation of symbols.

Fig. 2. Bean pods of different ages, all of the same susceptible variety, inoculated at the same time with one biologic form of *Colletotrichum lindemuthianum*. Very small brown lesions only were produced on the oldest pod altho it was still green and succulent. The specimens were taken from the experiment described in the text.

Fig. 3. A plant of Variety 20 inoculated with Culture 15 when eighteen days old. Note the complete susceptibility of epicotyl, while on the hypocotyl very small lesions only are produced. The same variety, inoculated when eleven days old, was completely susceptible.

S+ S   S—   R R—

FIGURE 1

FIGURE 2
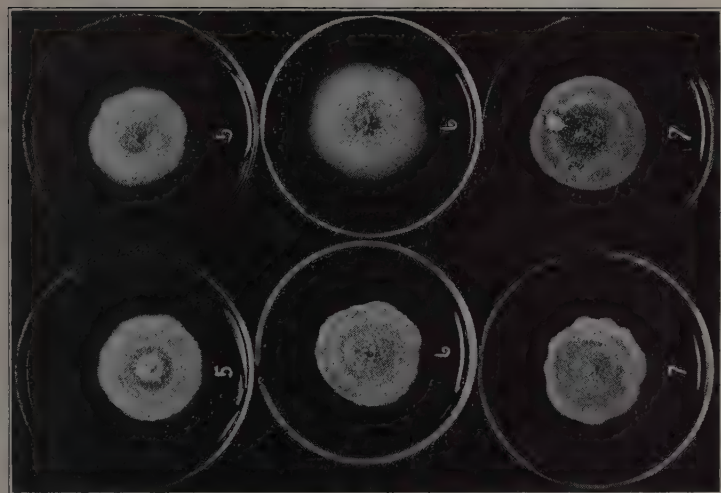

FIGURE 3

FIGURE 1

FIGURE 2
PLATE II

PLATE III

FIGURE II

FIGURE I

PLATE IV

Two Biologic Forms of *Colletotrichum lindemuthianum* Growing on Flasks of Modified Czapek's Solution Containing Carbohydrates as Indicated

Culture 6 grew fairly well on both solutions, while Culture 15 produced only a small quantity of mycelium which was abnormal in appearance.

PLATE VI

Stages in the Development of *Colletotrichum lindemuthianum* in Susceptible and Resistant Hosts

Fig. 1. A surface view of a piece of epidermis, stripped from a susceptible bean stem, showing stage of infection 52 hours after inoculation. The appressorium has been formed very close to the spore, penetration has occurred, and the large primary mycelium can be seen in three epidermal cells. No detrimental effects on the host protoplast or cell walls can be detected. x 420 (approx.)

Fig. 2. Infection and subsequent development of the primary mycelium as seen in cross-section of a susceptible bean stem 99 hours after inoculation. Observe the thickness of the mycelium in the epidermal cell and its adherence to the walls of the cortex cells. This is very probably due to the retarding of apical growth during the process of cell-wall penetration. Note also the very small hole through which penetration was effected. No swelling or discoloration of the cell walls could be detected. A composite drawing of three sections from a stained slide. A photomicrograph of one of the sections is shown in Plate VII, Fig. 2. x 1050 (approx.)

Fig. 3. Successive stages of cell-wall penetration as observed from living material in a cross-section of a stem of a susceptible variety. The section was cut free hand, 72 hours after inoculation, and mounted in distilled water. The position of the mycelium when it reached the point *a* is indicated by the dotted line. During penetration it bent slowly over to the wall of the cell, at the same time becoming slightly enlarged. It retained this position after penetration was accomplished and there was a distinct indentation of the cell wall that only partially disappeared. While the mycelium was penetrating at *b* it became distinctly wavy, as indicated by the dotted line, but straightened again after penetration had been effected. The two cell walls were split apart along the middle lamella during the process of penetration at *c*. For a more detailed description see the text. x 500 (approx.)
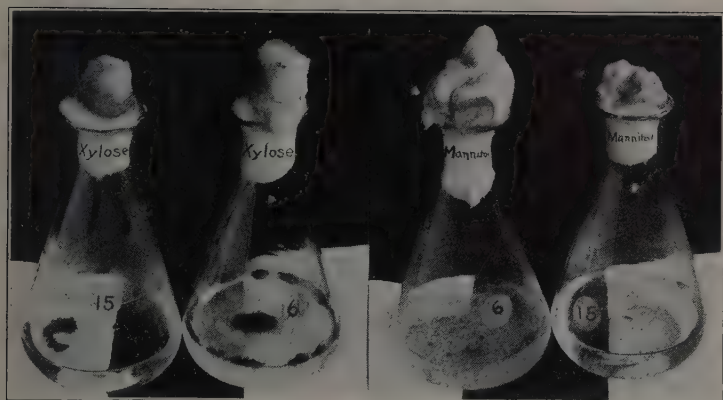
PLATE V

PLATE VI (*Continued*)

Fig. 4. Mycelium in two host cells of a susceptible variety as seen in a cross-section of a stem 99 hours after inoculation. The large primary mycelium has almost filled the cells in cross-section, crowding the protoplasts to one side. Notice that the organization of the host protoplast is yet intact. From a stained section 12 microns thick. x 1000 (approx.)

Fig. 5. A type of cell wall penetration by the primary mycelium occasionally found in which no bending occurs, but in which there is a permanent enlargement just over the point of penetration. x 1000 (approx.)

Figs. 6, 7, and 8. Three typical cases of cell wall penetration by the secondary mycelium as seen in sections of material killed 126 hours after inoculation. The cell walls have become softened and the small mycelium meets very little resistance. It penetrates through a large hole with almost no constriction and very little enlargement. x 1000 (approx.)

Fig. 9. A surface view of a piece of epidermis stripped from a resistant bean stem 72 hours after inoculation. Two cells have been penetrated. The walls and contents of both have been stained reddish brown. Both the mycelium and host protoplast show signs of disintegration. Compare with Plate VI, Fig. 1. x 500 (approx.).

Fig. 10. A portion of a cross-section of a stem of a resistant variety killed 83 hours after inoculation. The cell directly beneath the appressorium has collapsed and its cell walls and contents stain a homogeneous red with diamant fuchsin. In fresh material they are stained reddish brown. Two fragments of partly disintegrated mycelium can be seen in the second and third cells below the epidermis. These cells have not yet collapsed but the walls are becoming discolored, as indicated by their affinity for diamant fuchsin. x 1000 (approx.).

Fig. 11. A section similar to Fig. 10 with the exception that only one cell was penetrated by the fungus. x 1000 (approx.).
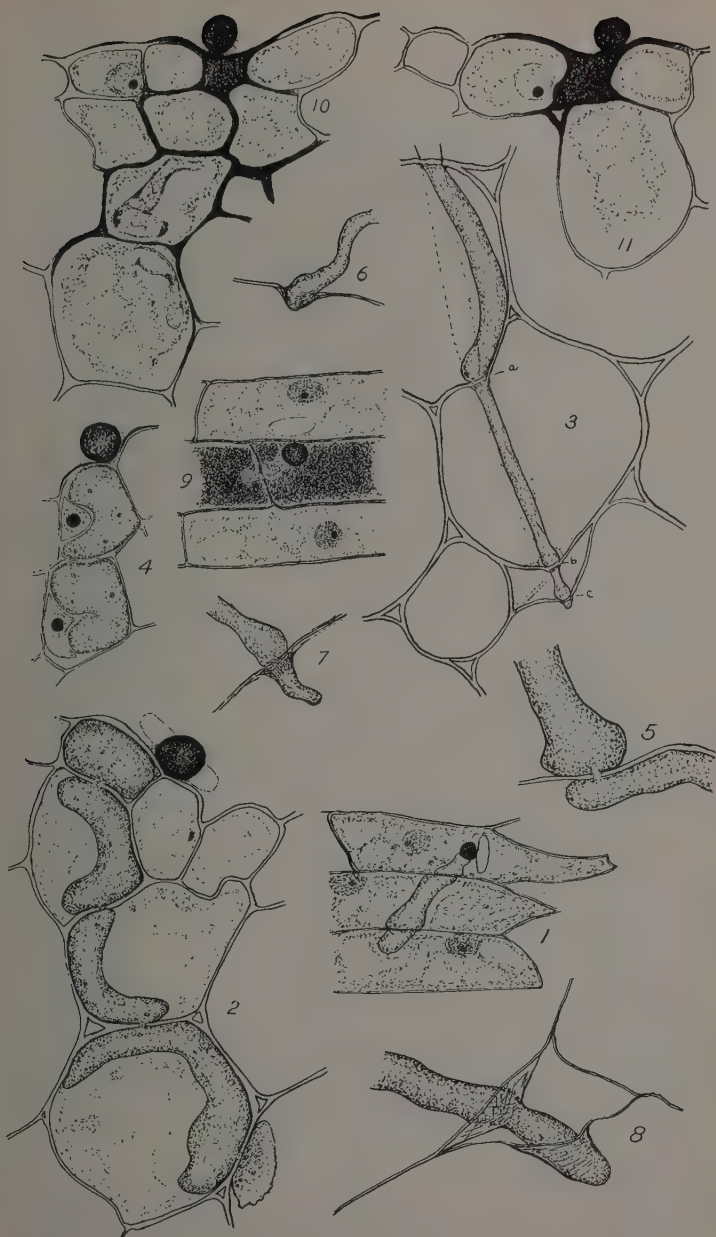
PLATE VI

Plate VII

Stages in the Development of *Colletotrichum lindemuthianum* in the Tissues of
a Susceptible Variety of Bean

Fig. 1. A free-hand section of a susceptible bean stem cut about 75 hours
after inoculation. Note the large primary mycelium lying against
the cell walls. No discoloration or disintegration of host protoplast
or cell wall could be detected at this point. The fungus was evi-
dently taking its nourishment from the host protoplast which was
yet alive. x 500 (approx.).

Fig. 2. Characteristic development of the primary mycelium. The adherence
of the hyphae to the cell wall is undoubtedly due to the bending
brought about by the resistance of the cell wall to penetration.
From a stained section slide. x 500 (approx.).

Fig. 3. A free-hand section of a susceptible bean stem, showing a hypha
bending during the process of cell wall penetration. x 250 (approx.).

Fig. 4. Infection of a susceptible stem and development of the primary
mycelium as seen in cross-section. From a stained slide of material
killed 99 hours after inoculation. The large primary mycelium is
found always in the early stages of infection of a susceptible variety.
x 600 (approx.).

Fig. 5. A typical example of cell-wall penetration by the secondary mycelium.
There is no constriction or enlargement of the mycelium at the
point of penetration. The wall has been penetrated at the corner of
the cell and the wall of the adjacent cell has been pushed aside,
indicating that the middle lamella has probably been dissolved. From
a stained longitudinal section of a stem killed 126 hours after
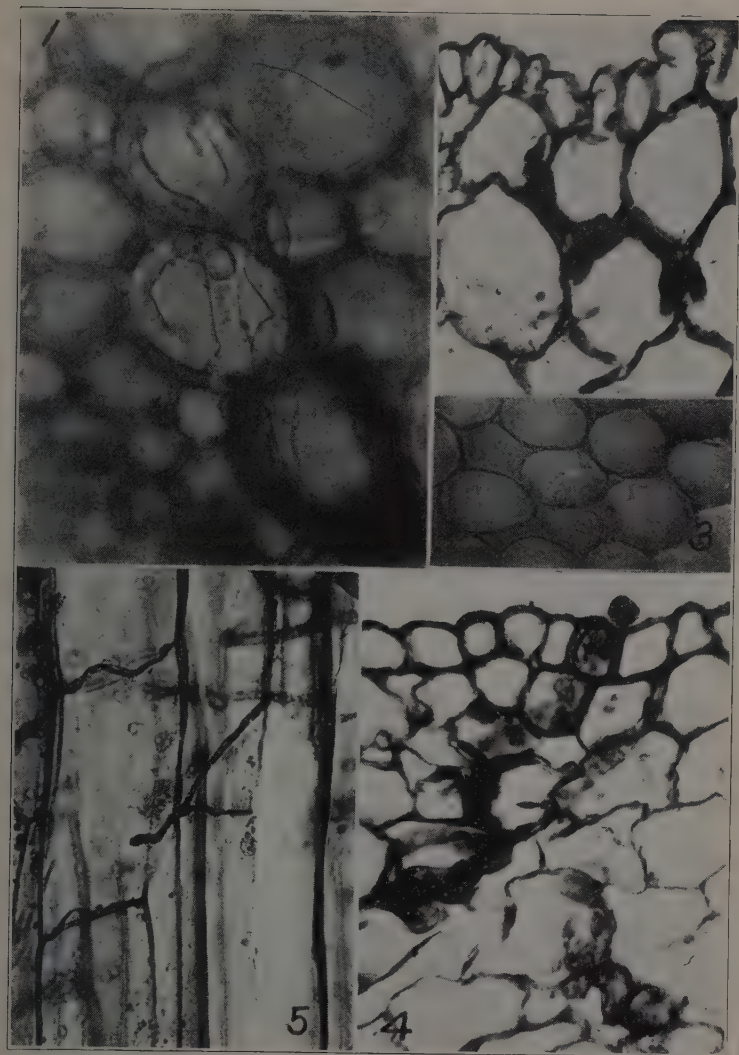inoculation. x 350 (approx.).

PLATE VII

Stages in the Development of *Colletotrichum lindemuthianum* in the Tissues of a Resistant Variety of Bean

Fig. 1. Cross-section of a stem of a highly resistant variety 83 hours after inoculation. The mycelium has advanced into two cells only, and is beginning to disintegrate. The walls of the epidermal cell have become slightly discolored and are beginning to collapse. From a stained slide. x 1200 (approx.).

Fig. 2. Section similar to that in Fig. 1 but more advanced. The mycelium and the protoplast of the attacked cells have completely disintegrated and the cell walls have collapsed. Both the walls and cell contents have been stained a homogeneous red by the diamant fuchsin. x 1000 (approx.).

Fig. 3. Cross-section of a lesion on a less resistant variety. The mycelium advanced some distance from the point of infection, but it has entirely disintegrated, causing also the destruction of the host cells. From a stained slide of material killed 160 hours after infection. x 100 (approx.).

Fig. 4. Disintegrating mycelium in a resistant variety 70 hours after inoculation. From a stained slide. x 350 (approx.).

Fig. 5. Cross-section of a stem of a resistant variety 83 hours after inoculation, in which the fungus has penetrated only one cell. The mycelium has disintegrated, staining the host-cell wall and protoplast. The cell wall has not yet collapsed. x 750 (approx.).

Fig. 6. Result of infection on a highly resistant variety, from a stained slide of material killed 83 hours after inoculation. The mycelium has disintegrated and the host cell has collapsed. The walls and entire contents have been stained a homogeneous red by the diamant fuchsin. The protoplasts of adjacent host cells are uninjured. x 750 (approx.).

PLATE VIII

The University of Minnesota
Agricultural Experiment Station

A Study of the Damping-off
Disease of Coniferous Seedlings

Division of Forestry and
Division of Plant Pathology
and Botany
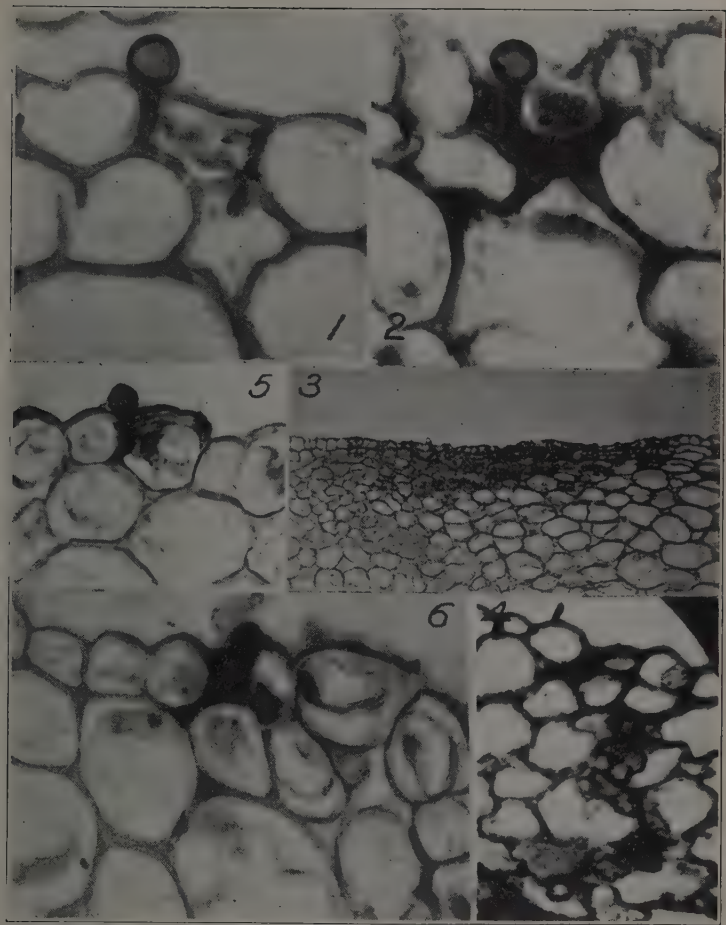
AGRICULTURAL EXPERIMENT STATION

ADMINISTRATIVE OFFICERS

The University of Minnesota
Agricultural Experiment Station

A Study of the Damping-off
Disease of Coniferous Seedlings

Division of Forestry and
Division of Plant Pathology
and Botany

CONTENTS

ILLUSTRATIONS

A STUDY OF THE DAMPING-OFF DISEASE OF CONIFEROUS SEEDLINGS

By T. S. Hansen, W. H. Kenety, G. H. Wiggin, and E. C. Stakman

INTRODUCTION

The fungi which attack young coniferous seedlings and which are commonly known as the "damping-off" disease, form one of the most serious obstacles encountered in the raising of such stock in the nursery. The frequency and severity of losses from this disease among very young nursery stock have attracted the attention of pathologists, nurserymen, and foresters for many years, both in this country and abroad. Some species seem to be more susceptible than others, but practically all coniferous species handled in nurseries in this country are affected.

Spaulding and Hartley have made several studies of the organisms which cause damping-off in this country. Spaulding found more than 40 species of Fusarium which would cause the damping-off of pine seedlings. Hartley showed that both Rhizoctonia and Pythium caused very severe injury in the nurseries in Nebraska, and through experiments he worked out a system of soil sterilization for the prevention and control of the disease that was successful to a marked degree.

Unfortunately, the large number of organisms causing the disease and the great variation in climatic and edaphic factors in different parts of the country, make measures which are effective in one part of the country almost useless in another. Organisms which cause trouble in one region may be wholly lacking in another. Moreover, observations made during several years at the Cloquet Forest Experiment Station would seem to indicate that methods of nursery practice have an important influence on damping-off.

In order to determine the best fungicides for use with the native species in the Norway-jack pine type of country, which forms such a large proportion of the forest area of the Lake states, a rather elaborate project was inaugurated at the Cloquet station in co-operation with the Division of Plant Pathology and Botany. Work on the project started in 1914 and was not completed till 1919

PART I. OUTLINE OF PROJECT

An outline of the project was drawn up to cover the following points, which were considered as having a possible bearing on the development of the damping-off fungi.

TIME OF SOWING

It was known that early and late sowing had a marked effect on the percentage of germination and the rate of development of seedlings, but no exact data had been obtained on their relation to damping-off. A series of experimental sowings was planned to cover every practicable sowing date.

PRELIMINARY TREATMENT OF SEED

It was thought that soaking the seed before sowing might, through its effect on the rate of germination, influence the percentage of injury from damping-off, and plots were planned to check this point.
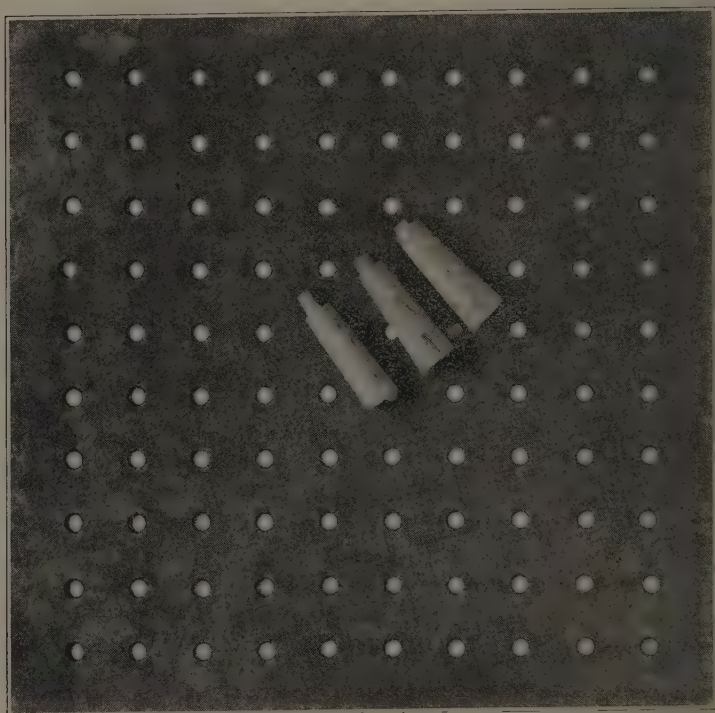
Fig. 1. Sheet Iron Plate Used in Planting Square-foot Plots

Plates with 100, 200 and 300 holes were used. One seed was put in each hole and pushed down the desired depth with one of the punches shown. Flanges on these punches regulated the depth. The seed were covered by rubbing soil over the plate. That which did not fall into the holes was scraped off. Uniformity in spacing and depth was thus secured.

Plots were also introduced to check the effect of: depth of cover applied to seeds in the seedbeds; use of common fertilizers; use of shade of different densities; application of different amounts of water; crowning of the beds for drainage; use of different fungicides and time and method of their application.

GENERAL PLAN

The general plan was as follows: Several standard beds, 4 x 12 feet, were laid out in a compact block in a corner of the nursery where the conditions would be as nearly uniform as possible. Except in the case of the test for drainage the beds were built in the regular way with a crown of one inch.

In each of these beds, 18 plots one foot square were laid off in three rows, as shown in Figure 2. In the first row the seed was planted 100 to the square foot, in the second row 200, and in the third row 300.

INFLUENCE of TIME of SOWING.
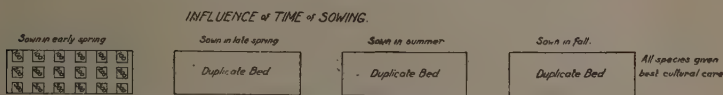
Fig. 2. Arrangement of Beds Used in Determining Influence of Time of Sowing

Uniformity of spacing and accurate density were obtained by means of three perforated iron plates such as that illustrated in Figure 1. One plate had 100 perforations, another 200, and another 300. The plate was placed accurately on the plot. A single seed was placed in each perforation and pressed in with a shouldered peg. Uniform depth of covering was obtained by scattering dirt over the plate and rubbing off the excess which did not go into the holes.

Whenever a check was needed, at least a third, often a half and in some cases two thirds of the plots were kept as a check plot, thus obtaining an accurate, geometrically distributed check. Every seedling in all the plots was considered in arriving at results. There were no arbitrary selections.

HISTORY OF PROJECT

In 1914-15 an attempt was made to secure data from beds sown in the routine way in the regular nursery. Differences due to lack of uniformity in spacing, depth of cover, drainage, etc., that always occur in general nursery practice, completely vitiated the results. The error occasioned by arbitrarily picking out certain beds, or parts of beds, for checks, without being sure of the absolute similarity of the cultural conditions of both checks and experimental plots, made the results even more unreliable.

In 1916 the project was carefully organized on a systematic basis. It was hoped to isolate the different factors and fix the responsibility for results. Even then results were not sufficiently conclusive on some of the points and the experiments in which results were doubtful were repeated in 1919. The 1916 experiments dealt exclusively with white, Norway and jack pine. The 1919 series included white spruce instead of jack pine.

The details of the whole series of experiments follow:

TIME OF SOWING

To determine the effect of the date of sowing on the rate and percentage of germination and the effect which these factors have on damping-off, plots were sown September 15, October 15, April 15, May 1, May 15, June 1, June 15, July 8 and July 15. Records were kept of the mean soil temperature from the time of sowing to the time of germination, and of the number of days required for germination in each case. The results are shown in Tables I and II. Figure 2 shows the arrangement of the beds.

TABLE I

EFFECT OF DATE OF SEEDING ON RATE OF GERMINATION

Species		Sept. 15	Oct. 15	April 15	May 1	May 15	June 1	June 15	July 8	July 15
Jack pine	Mean soil temperature from time of sowing				59.6	67.9	.....	69.2	.....	77.5
	Days for germination		215	35	25	16	..:..	15	.....	11
Norway pine	Mean soil temperature*	62.3	...:.	57	55.3	65.4	62.3	.....	69.9	.....
	Days for germination	40	.....	72	54	40	31	.....	17	.....
White pine	Mean soil temperature*	62.3	.....	57	55.6	65.4	62.3	.....	70	.....
	Days for germination	40	.....	73	61	40	34	.....	25	.....

* Temperatures were taken with a soil thermometer covered the same depth as the seed. Readings were taken at the same time each day, and averaged. The longer period of sunlight in June and the more direct incidence of the sun's rays and higher temperature on certain days in the latter part of May and June, account for the decrease in length of time for germination in these months. Fifteen days of high temperature in the last part of May averaged with 15 days of low temperature in the first part would shorten the germination period more than 30 days of even temperature in April which might give the same or a higher average. In May and June the nights are uniformly warmer.

Table I illustrates very clearly the direct relationship between soil temperature and the rapidity of germination. [1]

The results recorded in Table II show clearly that the percentage of damping-off among seedlings from seed sown in the summer is lower than among those from seed sown in the spring, especially with Norway pine. Little is known of the ecology of these fungi, but summer conditions are apparently adverse to their growth.

[1] The sowing late in the summer showed a higher percentage of germination, but the seedlings were very poorly developed at the end of the season.

TABLE II
EFFECT OF DATE OF SOWING ON DAMPING-OFF

Species	Early spring		Late spring		Summer	
	% Germination	% Damping-off	% Germination	% Damping-off	% Germination	% Damping-off
White pine.............	41.0	10.4	46.1	36.7	....	....
Norway pine............	71.7	23.3	82.6	28.6	97.0	5.0
Jack pine..............	67.0	17.0	76.0	8.0	76.0	7.0

PRELIMINARY TREATMENT OF SEED

Some coniferous seeds, especially those of white pine, do not germinate uniformly. The period of germination sometimes extends through two seasons and the rate is very irregular. It is a common practice to soak these seeds before sowing in order to hasten the rate of germination and make it more uniform.

To determine the result of this practice and its effect on damping-off, a series of plots was planted with seed which had been soaked one, two and four days, and careful data were collected on the percentage of germination and the comparative loss from damping-off.

Figure 3 shows the arrangement of the beds. The results are shown in Table III.

Fig. 3. Arrangement of Beds Used in Determining the Effect of Treatment of Seed Before Sowing

TABLE III
EFFECT OF PRELIMINARY TREATMENT OF SEED

Species	Days soaked									
	1		2		4		Average		Check	
	% Germ.	% D.O.	% Germ.	% D.O.	% Germ.	% D.O.	% Germ.	% D.O.	% Germ.	% D.O.
White pine.............	48.6	33.5	57.5	30.4	70.5	30.0	58.9	31.3	70.0	20.0
Norway pine..........	33.8	14.7	34.5	28.0	40.8	35.8	36.3	26.1	35.8	21.3

The effect of preliminary soaking on the germination of these two species seems to be very uncertain. With the exception of the four-

day soaking, the practice did not raise the percentage of germination, and with the single exception of a one-day soaking of Norway pine, the loss from damping-off was considerably increased.

DEPTH OF COVER

The depth to which seed is covered influences the length of time between the bursting of the seedcoat and the appearance of the seedling above ground. During this period and until the root system becomes established, the seedling derives its food from the seed. Therefore the shorter this period the sooner the plant can start photosynthetic activity and the more vigorous the seedlings should be. Preliminary work in 1914-15 with Norway and white pine indicated that the lighter the cover the less the damping-off. Further experiments were carried on in 1916 with these species, and were repeated in 1919 with white spruce included.

Figure 4 illustrates the arrangement of the beds in 1916. A similar arrangement was followed in 1919 except that white spruce was substituted for jack pine and a uniform number of seed, 200 per square foot, was sown throughout. Table IV gives the results.

TABLE IV
EFFECT OF DEPTH OF COVER

Depth of cover, Inches	White pine				Norway pine				Jack pine		White spruce*	
	1916		1919		1916		1919		1916		1919	
	% Germ.	% D. O.	% Germ.	% D. O.	% Germ.	% D. O.	% Germ.	% D. O.	% Germ.	% D. O.	No. Germ.	% D. O.
⅛	......	......	11.1	5.7	79.0	11.1	72.0	5.7	81.0	15.0	175	5.6
¼	46.0	9.1	13.8	8.1	82.4	10.7	67.0	8.3	75.0	16.0	147	2.7
½	42.0	18.7	13.6	14.6	......	......	60.5	14.2	......	......	51	4.0
¾	31.7	16.5	......	......	......	......	......	......	......	......	......	......
⅜	......	......	......	......	64.2	20.1	......	......	61.0	15.0	......	......

* In sowing the spruce in this experiment, it was found impossible to control the amount of seed, because of the small size and poor quality. Hence the germination is given in numbers per square foot.

EFFECT of DEPTH of COVER.

Sown to white pine.
Covered 4" Covered ½" Covered ¾"

Sown to Norway pine.
Duplicate Bed
Covered ⅛" Covered ¼" Covered ½"

Sown to jack pine
Duplicate Bed
Covered ⅛" Covered ¼" Covered ⅜"
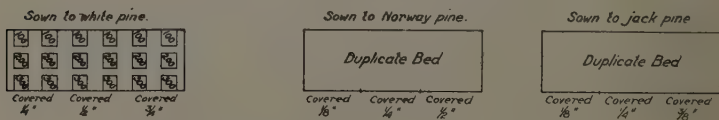
Fig. 4. Arrangement of Beds Used in Determining Effect of Depth of Cover

The figures in this table show that increase in depth of cover decreases germination and increases damping-off. White pine seems to be least affected by the depth of cover. A cover of ⅛ inch seemed too thin for good practice.

FERTILIZERS

The use of manure or other fertilizers affects the development of the seedlings and makes a radical difference in the growing conditions for the fungi. Previous work with acid phosphate and sodium nitrate showed a marked tendency to increase damping-off in the beds so treated. Manure and tankage, which both contain a large variety of plant foods, were selected for the experiments in 1916. Figure 5 shows the arrangement of the beds. Table V shows the results of the experiments.

EFFECT of FERTILIZERS
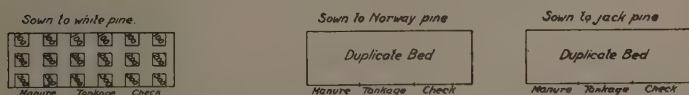
Fig. 5. Arrangement of Beds Used in Determining Effect of Fertilizers

TABLE V
EFFECT OF DIFFERENT FERTILIZERS

Fertilizer	White pine		Norway pine		Jack pine	
	% Germ.	% D. O	% Germ.	% D. O.	% Germ.	% D. O.
Manure.......	45.1	14.9	72.0	8.0	75.0	19.0
Tankage......	13.8	38.0	11.0	72.0	12.0	83.0
Check........	50.2	17.6	69.9	25.8	80.0	12.0

Tankage is clearly shown to reduce germination materially and to increase damping-off. The differences between the manured plots and the check plots were slight and variable. Further work must be done before any definite conclusions can be drawn.

SHADING

In order to determine the effect of different degrees of shade on the development and virulence of the organisms causing damping-off, plots were established in 1916 with three-fourths, one-half, and no shade. White, Norway and jack pine were used. Different plots were treated with different fungicides. Untreated check plots were, of course, maintained in every bed.

TABLE VI

EFFECT OF DEGREES OF SHADING

Treatment*	No shade 1916 % Germ.	% D.O.	% C.I.	No shade 1919 % Germ.	% D.O.	% C.I.	½ shade 1916 % Germ.	% D.O.	% C.I.	½ shade 1919 % Germ.	% D.O.	% C.I.	¾ shade 1916 % Germ.	% D.O.	% C.I.	¾ shade 1919 % Germ.	% D.O.	% C.I.
White pine—																		
⅜ Oz. H₂SO₄	42.1	9.8	0.0				59.5	10.3	1.7				47.1	5.3	0.3			
1:80 CHOH	38.3	35.6	1.3				54.3	8.5					41.1	14.1	0.4			
1:25 CuSO₄	39.3	1.2	68.2				51.0	11.7	1.0				45.3	5.5	33.4			
¼ Oz. H₂SO₄				6.2	24.0					9.5	2.6					13.0	11.5	
½ Oz. HCl				4.2	10.5					8.2	18.0					10.0	20.0	
1:40 CHOH				0.7						0.5		100				1.5		16.6
Check	36.2	28.3	0.7	27.4	21.3		50.4	18.2	0	13.2	8.0	5.0	41.7	14.2	0	14.5	13.7	0
Norway pine—																		
⅜ Oz. H₂SO₄	77.8	10.9	42.2				80.3	1.2	0.2				64.3	8.8	1.3			
1:80 CHOH	58.1	12.3	14.8				92.3	4.5	0.0				50.0	10.3	10.3			
1:25 CuSO₄			100.0				98.0	16.8	15.4						100.0			
¼ Oz. H₂SO₄				58.2	2.5					66.5	1.5	1.1				71.	2.8	
½ Oz. HCl				68.0	12.1					62.2	1.2					68.2	1.8	
1:40 CHOH				0.3		100				2.7		9.0				0		9.0
Check	72.3	26.2	1.0	60.4	3.7		85.5	16.7	0.0	67.4	11.2		82.1	17.4	1.1	61.7	11.7	1.1
White spruce—																		
¼ Oz. H₂SO₄				†3						†170	29.3					†19		
½ Oz. HCl				5						269	8.1	1.4				45	26.3	
1:40 CHOH				1	33.0					178	27.5	2.7				3	4.4	
Check				26						938	17.0					258	12.4	

*H₂SO₄ = Sulphuric acid.
CHOH = Formaldehyde.
CuSO₄ = Copper sulphate.
HCl = Hydrochloric acid.
† Number of seedlings per square foot.

These experiments were repeated in 1919, substituting white spruce for jack pine, changing some of the fungicides, and using a uniform density of 200 seeds per square foot. Figure 6 shows the arrangement of the beds in 1916. Table VI gives the results.

The 1916 series showed a larger amount of damping-off in the unshaded than in the shaded plots. This was true for both treated and untreated beds. The 1919 plots confirmed this conclusion, but not to such a marked degree. The spruce seed used in 1919 was of such poor quality that it was impossible to draw any definite conclusions in regard to that species.

Shading seemed to have little effect on the amount of chemical injury.

DEGREE of SHADING AFTER TREATMENT.
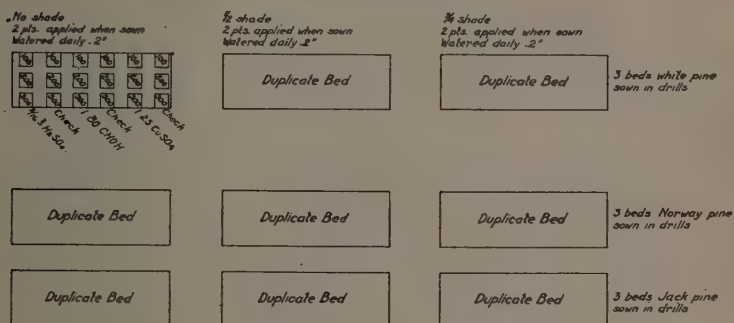
Fig. 6. Arrangement of Beds Used in Determining the Effect of Shading After Treatment

WATERING

In order to determine the effect of watering on the efficacy of the different fungicides, a series of plots was arranged as shown in Figure 7. The effect of watering on damping-off was studied in both treated and untreated plots. Watering was classified as light—one-half inch per week; medium—one inch per week; and heavy—two inches per week. Due allowance was, of course, made for the rain that fell. Table VII gives the results.

The amount of water did not seem to have any direct bearing on the effect of fungicides. During the first month after germination, the rainfall was quite uniform and heavy. In general, the heavy watering seemed to increase the amount of damping-off, but this did not hold true in every case, nor was the increase marked enough to be certain that it was the effect of the heavy watering.

This work was not continued in 1919 because it was strongly indicated in 1916 that enough water would be applied under general nursery practice to prevent concentration.
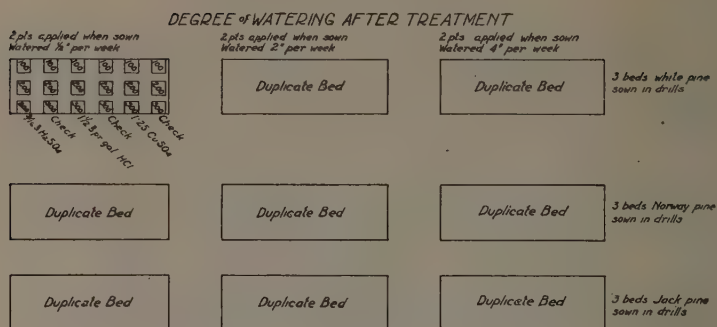
Fig. 7. Arrangement of Beds Used in Determining the Effect of Watering After Treatment

TABLE VII
EFFECT OF WATERING

Treatment*	Light			Medium			Heavy			None		
	% Germ.	% D. O.	% C. I.	% Germ.	% D. O.	% C. I.	% Germ.	% D. O.	% C. I.	% Germ.	% D. O.	% C. I.
White pine ⅜ Oz.												
H₂SO₄...	36.0	18.9	1.3	45.3	7.0	1.4	40.3	13.6	0	......	......	......
⅜ Oz. HCl....	46.0	14.4	1.1	47.6	11.9	0	49.3	19.2	0.3	......	......	......
1:25 CuSO₄...	45.3	9.2	24.6	48.8	9.5	17.7	46.0	9.0	38.0	......	......	......
Check...	......	......	...	......	......	......	......	......	......	33.1	26.2	0.2
Norway pine ⅜ Oz.												
H₂SO₄...	82.0	3.2	0.4	93.1	7.6	0.2	74.6	20.7	0.9	......	......	......
⅜ Oz. HCl.....	93.3	7.1	0.3	86.1	11.0	0.0	83.1	5.8	0.6	......	......	......
1:25 Cu SO₄..	79.0	3.1	88.4	73.8	2.5	92.1	90.6	7.5	82.7	......	......	......
Check...	73.0	26.7	0.4	74.2	27.0	......	77.7	29.7	5.0	......	......	......
Jack pine ⅜ Oz.												
H₂SO₄...	70.3	4.0	0	76.0	1.9	3.7	59.6	10.8	2.8	......	......	......
⅜ Oz. HCl.....	66.5	4.0	0	85.0	4.5	0	83.3	4.2	1.0	......	......	......
1:25 Cu SO₄.	32.8	2.0	8.3	60.1	0.3	92.	56.6	0.3	94.	......	......	......
Check..	46.5	19.0	0	45.1	17.	0.4	65.8	18.8	1.8	......	......	......

* H₂SO₄ =Sulphuric acid.
HCl =Hydrochloric acid.
Cu SO₄ =Copper sulphate.

MULCHING

To determine the effect of different mulches, applied immediately after sowing, on the development of damping-off disease a series of plots was arranged as shown in Figure 8. Table VIII shows the results.

A burlap mulch was beneficial on white pine, seemed to have very little effect on Norway pine, and was decidedly detrimental on jack pine. Sphagnum produced the highest germination in every case, and reduced the amount of damping-off except in the jack pine plots.

TABLE VIII

EFFECT OF MULCHES ON DEVELOPMENT OF DAMPING-OFF

Species	Mulch					
	Exposed		Sphagnum		Burlap	
	% Germ.	% D. O.	% Germ.	% D. O.	% Germ.	% D. O.
White pine....	53.7	21.8	59.9	16.6	55.4	15.3
Norway pine...	75.0	17.0	81.4	9.5	72.0	17.2
Jack pine......	78.0	10.0	79.0	15.0	73.0	22.0

EFFECT of DIFFERENT MULCHES.
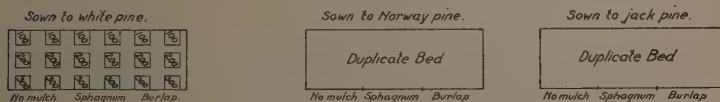
Fig. 8. Arrangement of Beds Used in Determining the Effect of Different Mulches

DENSITY OF SOWING

To determine the effect of the density of seedlings on damping-off, the results from all the 1916 beds, which were sown 100, 200 and 300 seeds to the square foot, were tabulated. The results for the jack pine beds are shown in Tables IX, X and XI. The results for the other species were similar.

TABLE IX

INFLUENCE OF DENSITY OF JACK PINE SEEDLINGS ON DAMPING-OFF IN TREATED BEDS

Bed No.	No. of seeds per square foot					
	100		200		300	
	Germ.	D. O.	Germ.	D. O.	Germ.	D. O.
31............	467	31	673	41	1253	43
32............	343	23	758	33	1386	58
33............	331	15	626	37	1122	61
34............	313	47	714	104	1227	108
35............	313	8	775	47	1314	85
36............	188	18	388	54	498	41
Total........	1955	142	3934	316	6800	396
Per cent......	54.3	7.2	54.6	8.0	62.9	5.8

TABLE X

INFLUENCE OF DENSITY OF JACK PINE SEEDLINGS ON DAMPING-OFF IN CULTURAL BEDS

Bed No.	No. of seeds per square foot					
	100		- 200		300	
	Germ.	D. O.	Germ.	D. O.	Germ.	D. O.
1.............	151	15	284	39	370	85
2.............	140	18	302	18	472	41
3.............	150	6	311	22	455	43
9.............	483	72	930	159	1354	212
12.............	341	39	903	133	1370	218
13.............	170	7	346	12	462	13
14.............	159	20	327	16	512	37
15.............	121	10	320	29	435	65
18.............	300	39	636	80	922	175
Total.........	2015	226	4359	508	6352	887
Per cent.......	71.6	11.2	77.8	11.6	75.6	13.9

TABLE XI

INFLUENCE OF DENSITY OF JACK PINE SEEDLINGS ON DAMPING-OFF IN CHECK PLOTS
OF TREATED BEDS

Bed No.	No. of seeds per square foot					
	100		200		300	
	Germ.	D. O.	Germ.	D. O.	Germ.	D. O.
31.............	233	10	421	26	668	30
32.............	152	15	306	16	648	38
33.............	160	39	244	26	476	48
34.............	145	16	336	13	607	48
35.............	135	3	357	30	624	56
36.............	92	16	147	42	255	36
Total.........	917	89	1811	158	3278	256
Per cent.......	50.9	9.7	50.3	8.7	60.7	7.8

The germination is from 4 to 8 per cent higher in the more
densely sown beds. Possibly this is because the larger number of
seeds break the crust and let the weaker seedlings through. There is
also, on the whole, less damping-off in the more thickly sown beds.

DRAINAGE

In order to determine the effects of drainage, a series of beds was
constructed which varied from each other only in the shape of the
surface. In some of the beds the surface was crowned up one inch

in the center, in others the surface was flat, and in still others the surface was hollow or sunken in the center, like the crowned bed inverted.

The arrangement of the beds is shown in Figure 9. The results are given in Table XII.

EFFECT of DRAINAGE of BEDS.
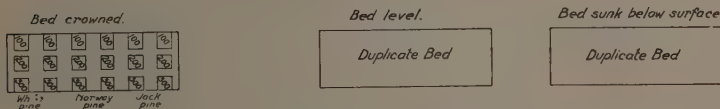
Fig. 9. Arrangement of Beds Used in Determining the Effect of Drainage

TABLE XII
EFFECT OF BED CONSTRUCTION ON DAMPING-OFF

Species	Crowned bed		Level bed		Sunken bed	
	% Germ.	% D. O.	% Germ.	% D. O.	% Germ.	% D. O.
White pine....	47.1	12.2	51.0	14.7	34.2	30.0
Norway pine...	87.5	17.1	83.9	10.1	70.3	31.0
Jack pine......	81.0	3.0	83.0	7.0	73.0	12.0

The crowned bed, which gives the best drainage, shows the least damping-off, except in Norway pine, and even there the difference is not so marked that the increase can be definitely attributed to the method of bed construction.

EFFECT of SOIL on FUNGICIDAL TREATMENTS.
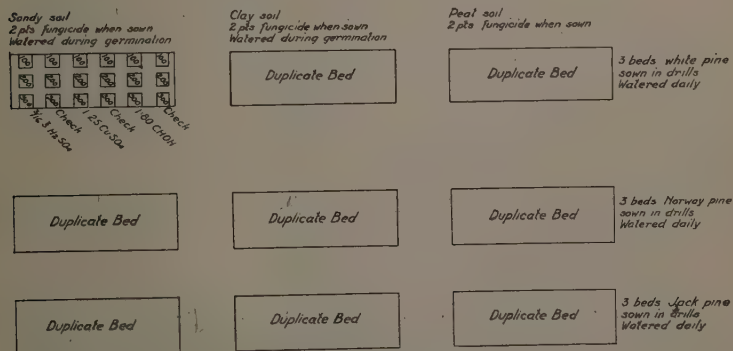
Fig. 10. Arrangement of Beds Used in Determining the Effect of Different Soils on Fungicidal Treatments

CHARACTER OF SOIL

To determine the effect of different kinds of soil a series of beds was arranged as shown in Figure 10 using sand, clay and peat soils. Unfortunately an accident destroyed the jack pine and white pine beds. The results for the Norway pine bed are given in Table XIII.

TABLE XIII

EFFECT OF KIND OF SOIL ON DAMPING-OFF OF NORWAY PINE SEEDLINGS

Treatment*	Clay			Peat			Sand		
	% Germ.	% D. O.	% C. I.	% Germ	% D O.	% C. I.	% Germ	% D. O.	% C. I.
$\frac{3}{8}$ oz. H_2SO, H_2O daily	36.3	10.1	73.0	65.0	5.1	0	74.6	20.7	0.9
1:25 $CuSO_4$, H_2O daily	56.0	33.6	32.4	56.3	13.0	10.0	90.6	7.5	82.7
1:80 CHOH, No H_2O	25.5	43.1	22.8	77.5	6.4	1.3	92.3	4.5	0
No treatment, No H_2O	36.0	41.9	4.0	82.1	12.0	0.6	85.5	16.7	0

* H_2SO_4 = Sulphuric acid.
$CuSO_4$ = Copper sulphate.
CHOH = Formaldehyde.
H_2O = Water.

Germination was lower in clay than in muck or sand, while damping-off and chemical injury are relatively higher in clay, except where copper sulphate was used. Copper sulphate caused a great deal more injury in sand, because there is a possibility of a greater concentration in sand than in either clay or peat.

FUNGICIDES

In order to determine the efficiency of different fungicides in a preliminary treatment of the soil before sowing, a series of plots was arranged as shown in Figure 11.

So little was known of the fungi that the fungicides were selected at random. All solutions were based on the application of a certain amount of fungicide per square foot. Water was considered only a medium for securing even distribution of the fungicide. Three different strengths were tried in 1916 of sulphuric acid, formaldehyde, copper sulphate, zinc chloride, hydrochloric acid, and lime-sulphur solution. The results are given in Table XIV.

Sulphuric acid, hydrochloric acid, and formaldehyde were the most effective. Copper sulphate, zinc chloride, and lime-sulphur were not nearly so effective as fungicides and caused more loss from chemical injury than there was from damping-off in the check plots.

TEST of FUNGICIDES.

Fig. 11. Arrangement of Beds Used in Testing Various Fungicides

TABLE XIV

EFFECT OF VARIOUS FUNGICIDES, 1916

Treatment* in 2 pints H₂O per square foot	White pine			Norway pine			Jack pine		
	% Germ.	% D. O.	% C. I.	% Germ.	% D. O.	% C. I.	% Germ.	% D. O.	% C. I.
H₂SO₄ ⅓ oz..................	51.8	10.6	0.6	81.6	2.0	0.2	60.8	5.8	0.8
H₂SO₄ ⅗ oz..................	59.5	10.3	1.7	80.3	1.2	0.2	54.8	3.0	0.6
H₂SO₄ ⅝ oz..................	57.0	12.6	0.0	62.1	3.0	0.8	63.1	4.8	·0.7
Check......................	49.8	19.4	0.6	85.5	16.7	0.0	73.0	5.0	0.5
CHOH 1:160.................	48.1	10.4	0.0	87.6	13.8	0.0	79.5	3.5	0.0
CHOH 1:120.................	59.6	8.1	0.0	90.0	6.5	0.0	74.8	3.3	0.2
CHOH 1:80..................	54.3	8.5	0.0	92.3	4.5	0.0	74.1	2.4	0.0
Check......................	50.4	18.2	0.0	88.7	10.9	0.0	62.0	5.6	0.0
Cu SO₄ 1:40................	48.3	20.7	1.0	89.6	17.1	18.4	74.8	4.6	26.5
Cu SO₄ 1:25................	51.0	11.7	1.0	98.0	16.8	15.4	67.3	6.1	62.5
Cu SO₄ 1:15................	52.3	7.0	3.4	91.0	16.4	34.4	51.0	2.0	72.5
Check......................	47.0	11.8	0.1	82.0	29.0	4.7	48.0	9.6	12.0
ZnCl₂ ⅓ oz.................	33.8	15.2	2.4	89.1	11.2	2.4	62.8	8.5	14.6
ZnCl₂ ⅓ oz.................	35.6	20.1	18.2	88.3	8.1	44.3	63.8	21.1	39.4
ZnCl₂ ⅝ oz.................	47.0	17.3	16.3	86.6	11.7	1.5	68.1	16.3	81.9
Check......................	41.4	20.5	1.8	83.7	37.0	1.9	57.0	7.6	9.5
HCl ⅜ oz..................	58.1	18.3	1.1	93.0	12.7	0.4	73.8	4.2	0.2
HCl ⅝ oz.	54.8	8.3	0.6	94.0	7.0	0.5	70.3	4.7	0.0
HCl ⅞ oz..................	55.5	8.7	2.1	90.0	3.7	0.4	73.6	3.8	0.2
Check......................	49.6	.18.5	0.5	87.0	23.7	0.1	61.0	7.7	0.0
Ca S 1:125.................	56.1	11.6	0.6	82.5	29.0	´3.2	22.0	1.5	11.3
Ca S 1:100.................	57.3	11.3	2.4	88.1	16.6	7.5'	24.3	2.7	18.0
Ca S 1:75..................	54.1	8.9	3.1	72.1	11.7	12.9	40.6	8.5	9.8
Check......................	50.2	22.2	0.5	81.5	13.4	0.4	27.0	7.8	3.4

* H₂SO₄ = Sulphuric acid.
  HCl = Hydrochloric acid.
  CHOH = Formaldehyde.
  Cu SO₄ = Copper sulphate.
  Zn Cl₂ = Zinc chloride.
  H₂O = Water.
  Ca S = Lime sulphur solution.

As the largest amounts of sulphuric acid, hydrochloric acid, and formaldehyde used in 1916 caused very little chemical injury, further experiments were tried with them in 1919, to determine the maximum strength usable and to provide a more complete sterilization of the soil.

Table XV gives the results of the 1919 experiments.

In this series the two acids proved more satisfactory. The stronger solutions, however, not only caused heavy chemical injury, but greatly reduced the percentage of germination. In White spruce the reduction of germination greatly exceeded the loss from damping-off in the check plots.

TABLE XV

EFFECT OF VARIOUS FUNGICIDES, 1919

Treatment* in 2 pints H₂O per square foot	White pine			Norway pine			White spruce		
	% Germ.	% D. O.	% C. I.	% Germ.	% D. O.	% C. I.	No. Germ.	% D. O.	% C. I.
⅛ oz. H₂SO₄	9.7	5.0	.....	71.0	1.4	1.0	267	31.8	.....
¼ oz. H₂SO₄	9.5	2.6	.....	66.5	1.5	1.1	170	29.3	.....
1 oz. H₂SO₄	9.2	.....	18.9	13.0	5.7	46.1	58	3.4	1.5
Check	13.2	8.0	.....	67.4	11.2	.....	938	17.0	.....
¼ oz. HCl	10.2	10.0	.....	60.7	1.6	.....	391	37.3	.....
½ oz. HCl	18.2	18.0	.....	62.2	1.2	.....	269	8.1	1.4
1 oz. HCl	6.7	.....	.....	26.5	6.6	4.7	187	19.2	10.1
Check	11.3	11.0	.....	62.0	6.0	.....	914	21.2	.....
1:80 CHOH	3.0	.....	8.0	10.7	4.6	.....	277	7.2	1.4
1:40 CHOH	0.5	.....	100.0	2.7	.....	9.0	178	27.5	2.7
1:20 CHOH	0.0	.....	.....	0.0	.....	.....	34	.....	20.5
Check	12.8	11.0	.....	64.4	5.5	.....	1107	8.0	.....

* H₂O = Water.
H₂SO₄ = Sulphuric acid.
HCl = Hydrochloric acid.
CHOH = Formaldehyde.

TIME OF APPLICATION OF FUNGICIDES

To determine the best time for applying the fungicides, a series of experiments was planned in 1916 using sulphuric acid and zinc chloride and formaldehyde.

Figure 12 shows the arrangement of the beds and Table XVI the results of the experiments.

TIME of APPLICATION of FUNGICIDES.
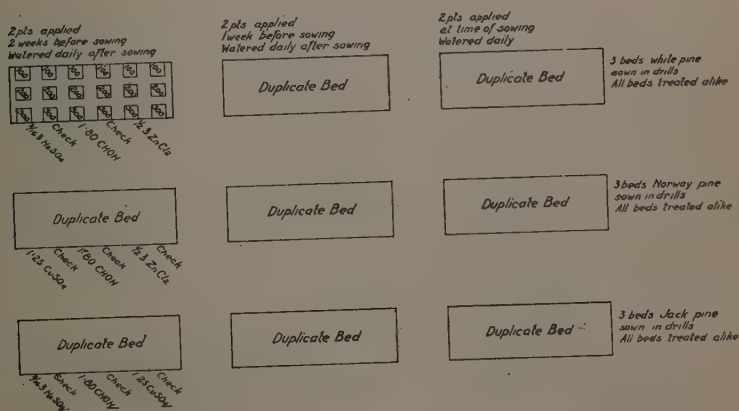
Fig. 12. Arrangement of Beds Used in Determining the Best Time for the Application of Fungicides

TABLE XVI

Effect of Time of Application of Fungicides

Treatment* in 2 pints H₂O per square foot	2 weeks before sowing			1 week before sowing			At time of sowing		
	$\%$ Germ.	$\%$ D. O.	$\%$ C. I.	$\%$ Germ.	$\%$ D. O.	$\%$ C. I.	$\%$ Germ.	$\%$ D. O.	$\%$ C. I.
White pine—									
⅝ oz. H₂SO₄	33.8	6.4	.....	32.5	9.7	0.0	29.8	16.2	0.0
1:80 CHOH	29.1	7.4	5.1	35.5	16.9	0.0	38.3	31.7	0.9
⅛ oz. ZnCl₂	32.5	9.2	1.0	41.0	22.7	1.2	37.0	28.0	7.7
Check	.....	.....	.....	.....	.....	.....	29.1	23.6	0.4
Norway pine—									
Cu SO₄	91.2	0.0	98.0	61.8	0.0	100.0	17.0	0.0	100.0
1:80 CHOH	84.0	7.5	0.0	81.6	16.7	0.0	34.6	49.0	0.0
⅛ oz. ZnCl₂	58.5	8.5	1.4	80.0	12.4	1.8	61.5	23.0	0.0
Check	.....	.....	.....	.....	.....	.....	65.3	25.4	0.3
Jack pine—									
⅝ oz. H₂SO₄	51.0	9.0	0.0	57.0	16.0	0.0	35.0	3.5	0.0
1:80 CHOH	66.0	10.6	6.0	46.0	13.0	1.0	24.0	100.0	0.0
⅛ oz. ZnCl₂	59.0	1.0	93.0	†	0.0	100.0	†	0.0	100.0
Check	.....	.....	.....	.....	.....	.....	49.0	11.0	0.0

* H₂O = Water.
 H₂SO₄ = Sulphuric acid.
 CHOH = Formaldehyde.
 ZnCl₂ = Zinc chloride.
 CuSO₄ = Copper sulphate.
 † Normal.

The plots treated in advance of sowing show a higher rate of germination, and, except in the case of jack pine, considerably less damping-off. The difference in chemical injury was negligible.

SPRAYING

In 1919 a series of plots was established to determine the efficiency of spraying with sulphuric acid, hydrochloric acid, and formaldehyde in preventing infection from the aerial spores of Fusarium.

The beds all received a soil treatment based on the results of previous work. White pine, ¼ oz. sulphuric acid per square foot; Norway pine, ½ oz. hydrochloric acid per square foot; white spruce, ¼ oz. hydrochloric acid per square foot.

In addition to the treatment of the soil, a spray solution was applied after the seed had begun to germinate. The spray used varied in strength as indicated in Table XVII. No definite amount of the spray was applied, but the plots were sprinkled lightly with the solution of different strengths.

Table XVII shows the effect of spraying with fungicides.

TABLE XVII

Effect of Spraying with Fungicides

Spray treatment*	White pine			Norway pine			White spruce		
	% Germ.	% D. O.	% C. I.	% Germ.	% D. O.	% C. I.	No. Germ.	% D. O.	% C. I.
¼ oz. H₂SO₄ per gallon..........	3.2	13.0	......	58.2	0.3	11.4	316	......	15.5
1 oz. H₂SO₄ per gallon..........	1.5	......	66.6	63.7	......	72.9	220	......	78.0
4 oz. H₂SO₄ per gallon..........	4.7	5.2	73.0	50.5	0.4	99.0	223	......	100.0
Check.........................	5.3	14.0	......	71.8	5.5	......	859	13.2	......
½ oz. HCl per gallon..........	11.0	......	4.5	68.2	......	8.0	210	4.0	22.3
2 oz. HCl per gallon..........	12.0	4.1	14.5	53.2	0.9	84.9	68	......	75.0
8 oz. HCl per gallon..........	3.0	......	92.0	51.7	......	100.0	173	......	99.0
Check.........................	9.8	10.1	......	81.8	2.2	......	700	16.2	......
1 oz. CHOH per gallon.........	10.7	2.3	4.6	66.0	......	97.7	268	......	88.0
2 oz. CHOH per gallon.........	9.0	5.8	27.7	58.7	......	99.1	31	......	77.4
4 oz. CHOH per gallon.........	8.5	......	41.2	47.2	......	98.3	189	......	94.7
Check.........................	7.2	6.9	1.1	80.3	6.9	14.1	860	6.2	......

* H₂SO₄ = Sulphuric acid.
  HCl = Hydrochloric acid.
  ·CHOH = Formaldehyde.

The weaker solutions had very little effect on damping-off. The stronger solutions caused disastrous chemical injury. In almost every case the combined loss from chemical injury and damping-off exceeded the loss from damping-off in the untreated check plots.

AGE AT WHICH SEEDLINGS ARE MOST SUSCEPTIBLE TO DAMPING-OFF

In order to keep an accurate record of the life history of the seedlings, each week's germination was marked with a colored toothpick stuck in the ground beside it. A different color was used for each count. By this means it was possible to tell the exact age of the seedling when it was affected with damping-off.
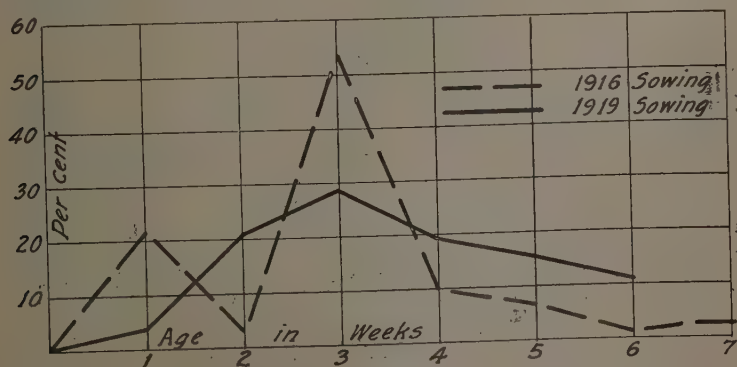
Fig. 13. Rate of Damping-off in Norway Pine
Average of all plots, both treated and untreated

Figures 13 to 20 show the behavior of the seedlings in general, and under separate treatments.

These curves show clearly that the critical period in the life of the seedling is the first four weeks. After this they are practically safe from damping off. In most cases the use of a fungicide seems to reduce the development of the disease, but to extend the period of its virulence.

Fig. 14.   Rate of Damping-off in White Pine,
Average of all plots, both treated and untreated

Fig. 15.   Rate of Damping-off in Jack Pine
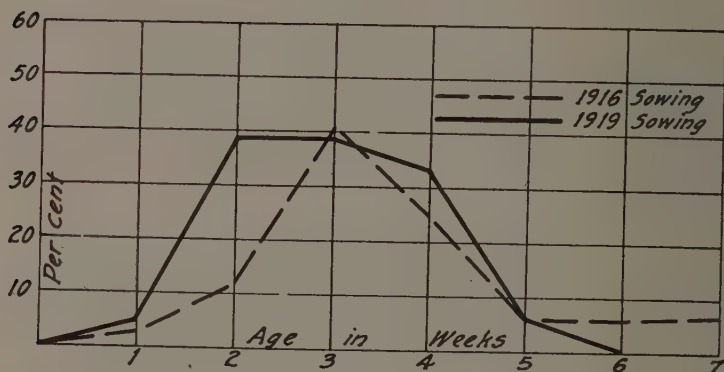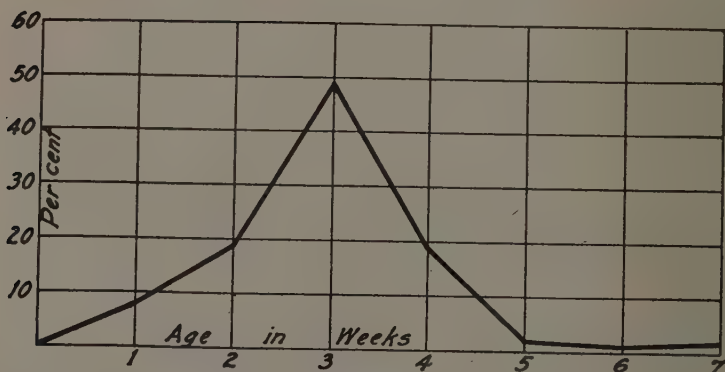Average of all plots, both treated and untreated
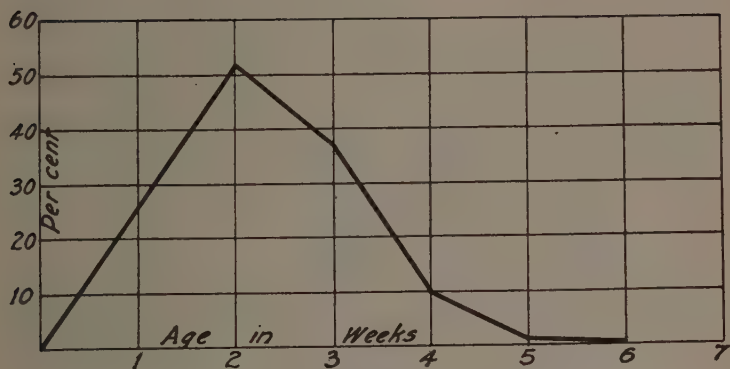
Fig. 16. Rate of Damping-off in White Spruce
Average of all plots, both treated and untreated
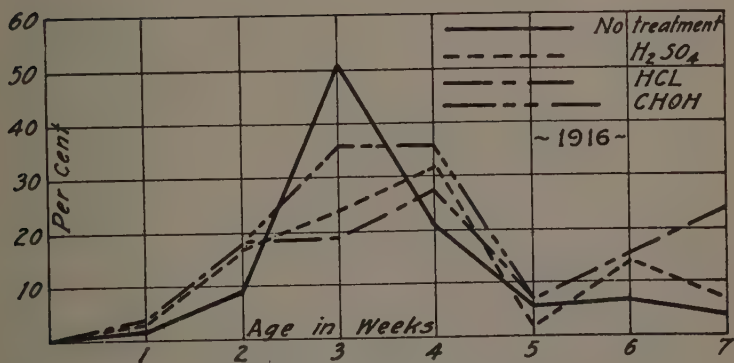
Fig. 17. Rate of Damping-off in White Pine
Each treatment given separately
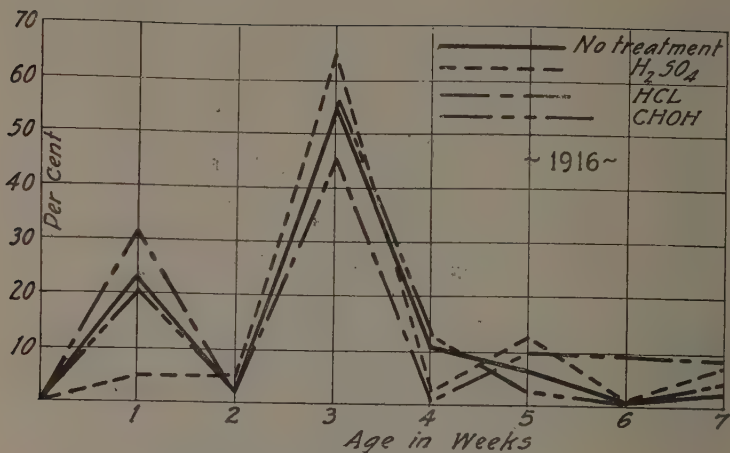
Fig. 18. Rate of Damping-off in Norway Pine
Each treatment given separately
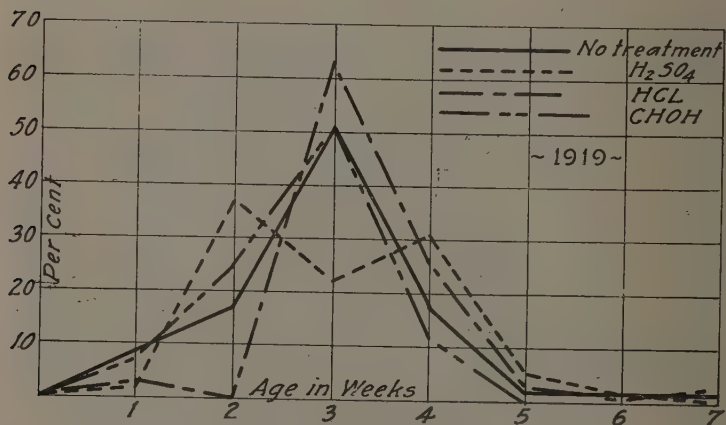
Fig. 19. Rate of Damping-off in Jack Pine
Each treatment given separately
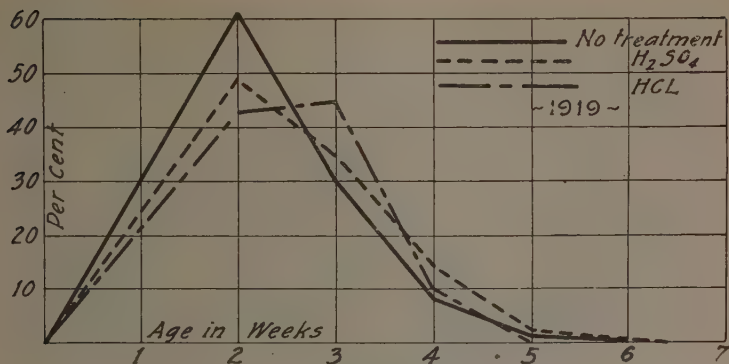
Fig. 20. Rate of Damping-off in White Spruce
Each treatment given separately

GENERAL SUMMARY OF CONCLUSIONS

1. To obtain rapid germination, seed should not be sown until the soil termperatures are above 60 degrees F. Too late planting, on the other hand, produces poorly developed seedlings at the end of the first season.

2. Seed sown in the early summer is much less subject to damping-off than that sown in the early spring. Late spring would seem to be the most satisfactory time, all things considered.

3. Preliminary soaking of the seed of white and Norway pine does not markedly hasten or increase the rate of germination. It does increase the injury from damping-off. It should not be practiced.

4. Increase in depth of cover decreases germination and increases damping-off. The seed should be covered as lightly as is consistent with good nursery practice.

5. Manure can be used as a fertilizer without increasing damping-off. Tankage decreases germination and increases damping-off. It should not be used.

6. Half shade gives the best results and there is no advantage in removing the shades after each rain.

7. The amount of watering does not materially affect the amount of injury from damping-off or from chemical treatment. The water called for by the best nursery practice may be applied without danger.

8. The use of sphagnum moss as a mulch increases germination and decreases damping-off with the possible exception of Jack pine.

9. The more densely seeds are sown—up to 300 per square foot, the higher the germination and the less the injury from damping-off.

10. A crown of one inch in the surface of the bed improves drainage and decreases the amount of damping-off.

11. Germination is lower, and both damping-off and chemical injury are higher in clay than in either peat or sand.

12.   The following are the best treatments for the sterilization of seedbeds and should be applied at the time of sowing: For white pine, ¼ ounce sulphuric acid per square foot; for Norway pine and white spruce, ½ ounce hydrochloric acid per square foot; for jack pine, 7/16 ounce hydrochloric acid.

13.   The application of any fungicide greatly reduces the germination of white spruce. The use of fungicides with this species is questionable.

14.   The expense of applying fungicides in advance of sowing is too great and the results are not worth while.

15.   No satisfactory spray for the control of Fusarium has yet been found.

16.   There is no great danger of loss from damping-off after the seedlings are four weeks old.

17.   Before any satisfactory methods can be worked out for the control of damping-off, the life history and ecology of the fungi causing the disease must be fully worked out.

PART II. FUNGI CAUSING DAMPING-OFF OF CONIF-
EROUS SEEDLINGS IN MINNESOTA

By E. C. STAKMAN [1]

INTRODUCTION

It is well known that under proper environmental conditions many different species of fungi may cause damping-off of coniferous seedlings. Those species, however, which are the most important in one locality may not always be the most important in other localities. It is known that different fungi react differently to the physical and chemical environment. It is very desirable, therefore, in conducting experiments on the control of damping-off to know what particular fungi are the most important in causing the disease, and which are the most resistant to the control measures applied. It should also be known whether the different species of fungi attack all species of conifers equally, or if certain fungi attack certain conifers more vigorously than they attack others.

The objects of the work reported below were as follows:

1. To ascertain what fungi are responsible for damping-off of coniferous seedlings in Minnesota.

2. To determine whether the same fungi attack all species of conifers equally.

3. To determine whether there was any correlation between the symptoms produced and the kind of fungi causing them.

4. To determine the resistance of the various fungi to soil treatment.

5. To determine which species of fungi were principally responsible for reinfestation of treated soil.

FUNGI FOUND ASSOCIATED WITH THE DISEASE

During August and September, 1916, isolations were made from 205 diseased seedlings. The fungi obtained from these plants are listed in Table I.

In 1919 another lot of seedlings was examined and the same fungi were found in approximately the same proportion. It will be observed that species of Fusarium, Pythium, Rhizoctonia, Alternaria, and Botrytis were the fungi most commonly present in the diseased seedlings. Species of Fusarium were especially common, having been isolated from 48.8 per cent of the plants examined in 1916. Pythium was second in frequency of occurrence, having been isolated from 35 per cent of the plants. Rhizoctonia was third and was found in 15.7

[1] L. L. De Flon, Miss Elsa Horn and J. L. Seal worked at various times on this phase of the project.

per cent of the plants. Alternaria was fourth and Botrytis fifth in order of prevalence. Often several of the above mentioned fungi were isolated from the same diseased seedling; 29 per cent of the specimens examined were infected with more than one species. The most frequent combination was that of Fusarium and Alternaria. These fungi were found associated in 13 per cent of the specimens examined.

TABLE I

FUNGI FOUND ASSOCIATED WITH DISEASED SEEDLINGS AT THE CLOQUET FOREST EXPERIMENT
STATION, 1916

Fungus	No. of seedlings attacked	Percentage of seedlings attacked
Fusarium...........................	54	26
Pythium	29	14
Rhizoctonia.......................	26	13
Alternaria.........................	7	3
Fusarium and Pythium..............	24	12
Rhizoctonia and Alternaria..........	6	3
Rhizoctonia and Pythium............	4	2
Pythium and Alternaria.............	2	1
Fusarium and Rhizoctonia...........	3	1
Fusarium and Alternaria.............	12	6
Fusarium, Pythium, and Alternaria....	1	$\frac{1}{2}$
Fusarium, Pythium, and Rhizoctonia....	2	1
Fusarium, Rhizoctonia, and Alternaria..	3	1
None...............................	30	15
Doubtful...........................	2	1
		. 99½

HOST RANGE OF THE FUNGI CAUSING DAMPING-OFF

An attempt has been made to find out whether any of the fungi were particularly virulent on certain kinds of seedlings. Altho fairly extensive observations were made, the indications are that the fungi causing damping-off are not restricted to any particular species of conifer. Fusarium, Pythium, and Rhizoctonia were commonly found on Norway, white and jack pine in the nurseries. In the greenhouse Fusarium and Botrytis were commonly found on Scotch and jack pine and also on blue and white spruce. A summary of the observations made in 1916 and 1919 is given in Table II.

TABLE II
Hosts Attacked by Various Fungi

Fungus	Norway pine 1916		1919		Jack pine 1916		1919		White pine 1916		1919	
	No. Pl.	Pct.	No. Pl.	Pct.	No. Pl.	Pct.	No. Pl.	Pct.	No. Pl.	Pct.	No. Pl.	Pct.
Fusarium	16	24	7	31	3	12	1	8	52	34	14	35
Pythium	2	3	1	5	6	25	4	34	15	9	4	10
Rhizoctonia	14	21	5	20	....	....	....	....	19	12	11	28
Alternaria	10	15	3	13	1	4	1	8	5	3	....	....
Fusarium and Pythium	....	....	1	5	....	....	....	....	14	9	5	13
Rhizoctonia and Pythium	....	....	....	....	....	....	....	....	6	4	1	3
Rhizoctonia and Alternaria	3	5	1	5	1	4	1	8	3	2	1	3
Fusarium and Alternaria	4	6	3	13	1	4	1	8	4	3	....	....
Rhizoctonia, Alternaria, Fusarium	....	....	....	....	....	....	....	....	1	....	1	3
Fusarium, Pythium, Alternaria	....	....	....	....	....	....	....	....	....	....	....	....
Rhizoctonia, Pythium, Fusarium	....	....	....	....	....	....	....	....	2	1	....	....
Doubtful	....	....	....	....	....	....	....	....	2	1	....	....
Nothing	17	26	2	8	12	50	4	34	31	20	2	5
Total	66	....	23	....	24	....	12	....	154	....	39	....

RELATION OF FUNGI PRESENT TO SYMPTOMS PRODUCED

The appearance of seedlings infected with damping-off is not always the same. Often the seedlings may be completely destroyed before they come through the ground. Again the plants may be attacked after they have emerged, but the entire plant will be completely destroyed. One of the most common types, however, is that in which the stem is attacked only at the ground line, the roots and lower stem being destroyed while the upper part of the stem is not attacked until after the plant has fallen. In some cases there is a general wilting of the entire plant and it soon dries up but remains standing. Often when older plants are attacked the roots are destroyed while the rest remains free of fungous infection until after the plant is dead. Frequently when the plants are not killed at once the stems become more or less swollen. Many minor variations of these symptoms have been observed. It is only reasonable to suppose that different fungi might consistently bring about more or less characteristic symptoms. However, a summary of the observations made in 1916 does not substantiate this view. There appears to be no appreciable correlation between the effect of the disease on the plant and the particular fungus causing the disease. A summary of these observations is given in Table III.

TABLE III

Fungi Found Associated with Diseased Seedlings Manifesting Different
Types of Injury, 1916

WHITE PINE

Dried, standing, swollen type. I C 2.

Fungus	No. seedlings attacked	Percentage
Fusarium	14	36
Pythium	4	10
Rhizoctonia	11	28
Rhizoctonia and Pythium	1	3
Fusarium and Pythium	5	13
Rhizoctonia and Alternaria	1	3
Fusarium, Rhizoctonia, and Alternaria	1	3
Nothing observed	2	5
	39	101

Bent seedling, D. O. below the leaves. II C 3a.

Fungus	No. seedlings attacked	Percentage
Fusarium	8	53
Pythium	1	7
Rhizoctonia	0	..
Fusarium and Pythium	2	13
Fusarium and Alternaria	2	13
Doubtful	1	7
Nothing observed	1	7
	15	100

Disease	No. seedlings attacked	Percentage
Bent seedling, D. O. all the way. II C 3b.		
Fusarium	6	50
Pythium	1	8
Fusarium and Pythium	3	25
Rhizoctonia and Pythium	1	8
Rhizoctonia, Alternaria, and Fusarium	1	8
	12	99
Limp, swollen type. II C 2.		
Fusarium	0	..
Rhizoctonia and Pythium	1	25
Fusarium and Pythium	1	25
Fusarium, Pythium, and Alternaria	1	25
Nothing observed	1	25
	4	100
Apparently dried, swollen type except that upper stem is green and softer. I C 2^1.		
Pythium	1	50
Fusarium and Pythium	1	50
	2	100
Standing but stem soft and flabby. I C 2^2.		
Rhizoctonia, Pythium, and Fusarium	2	100
Straight stem with D. O. below leaves. II C 4.		
Fusarium	2	100
Apparently dried, swollen type but fallen. I C 3^1.		
Fusarium and Alternaria	1	100
D. O. at groundpoint, stem above is normal. I C 3.		
Alternaria	1	100
Leaves only apparently D. O., stem dried. I. C. 2^3.		
Pythium and Alternaria	1	100

NORWAY PINE

Dried, standing type, not swollen. I A 1.		
Fusarium	7	30
Pythium	1	4
Rhizoctonia	5	22
Alternaria	3	13
Fusarium and Pythium	1	4
Fusarium and Alternaria	3	13
Rhizoctonia and Alternaria	1	4
Nothing observed	2	9
	23	99

Fungus	No. seedlings attacked	Percentage
Dried, standing type, swollen. I A 2.		
Rhizoctonia	2	29
Alternaria	1	14
Fusarium and Pythium	..	..
Fusarium and Alternaria	1	14
Rhizoctonia and Alternaria	3	43
	7	100
Apparently dried type but fallen. I A 1¹.		
Fusarium	1	50
Fusarium and Alternaria	1	50
	2	100
Apparently dried with green stem, slightly soft. ¹a, 1b.		
Doubtful	1	100
More or less limp but standing. I A 1b¹.		
Fusarium and Alternaria	1	100
Fallen, limp, and soft. II A 2.		
Fusarium	1	100
D. O. at groundpoint, stem above ground. I A 1a.		
Fusarium	1	100
Pythium	4	36
JACK PINE		
Dried, standing type. I B 1.		
Alternaria	1	9
Fusarium and Alternaria	1	9
Rrizoctonia, Alternaria, and Fusarium	1	9
Nothing observed	4	36
	11	99
Apparently dried type but fallen. II B 2.		
Fusarium	1	100

In 1919 isolations were made from a large number of seedlings manifesting many distinct types of injury, but no correlation could be made between the types of injury and the fungi causing them.

Altho excellent control was obtained by chemical treatment, a small amount of damping-off occurred in the treated beds. From the results of the isolations which are summarized in Table IV it can be seen that Fusarium, Pythium, Rhizoctonia, and Alternaria occurred in soil after treatment, but in about the same relative proportion in which they occurred prior to treatment. This does not justify the assumption that any of the fungi causing damping-off are to any great extent more resistant to the treatment than others. It is recognized here that it is entirely possible that many of the fungi found in the treated beds may have been due to reinfestation from outside sources, since no precautions were taken to prevent this.

FUNGI WHICH SURVIVE TREATMENT

TABLE IV

Fungi Isolated from Diseased Seedlings Grown on Chemically Treated Soil in 1916

	Upper stem	Lower stem	Total	Per cent
Fusarium..	35	40	75	30
Pythium..	13	9	22	9
Rhizoctonia..	17	16	33	13
Alternaria..	7	8	16	6
Fusarium and Pythium............................	10	4	14	5
Rhizoctonia and Pythium.........................	2	4	6	2
Rhizoctonia and Alternaria.......................	4	3	7	3
Fusarium and Alternaria..........................	6	2	8	3
Rhizoctonia, Alternaria, and Fusarium............	1	0	1	1
Fusarium, Pythium, and Alternaria...............	1	0	1	1
Rhizoctonia, Pythium, and Fusarium..............	1	1	2	1
Doubtful...	2	2	4	2
Nothing..	28	35	63	21
	..	..	..	99

SUMMARY

1.   The damping-off of coniferous seedlings in Minnesota is due to facaltative parasites found more or less universally in the soil, such as Fusarium, Pythium, Rhizoctonia, Botrytis, and possibly Alternaria. They are here given in the order of their prevalence.

2.   The fungi mentioned are often associated on the same host plant.

3.   Nothing conclusive has been found to show that one host species is more susceptible to an organism than another host species to the same organism.

4.   The different types of injury could not be correlated with the presence of the different kinds of fungi found in the lesions.   Each kind of fungus acting alone or in combination with other forms apparently can cause any or all of the different symptoms.

5.   All the organisms except Botrytis were found in beds that had been previously treated.   They were much less abundant than before treatment but in about the same relative proportions.

The University of Minnesota
Agricultural Experiment Station

Sunflower Rust

By D. L. Bailey
Division of Plant Pathology and Botany

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The University of Minnesota
Agricultural Experiment Station

Sunflower Rust

By D. L. Bailey
Division of Plant Pathology and Botany

CONTENTS

SUNFLOWER RUST

By D. L. Bailey[1]

INTRODUCTION

Altho the sunflower has been grown for a long time in this country for ornamental purposes, it is only recently that the economic value of the plant itself has been recognized. The seed is important as a source of a highly prized edible oil and of an oil cake rich in nitrogenous matter. Preliminary tests in Nebraska, Colorado, Montana, and Michigan have established also the desirability of sunflower silage and indicate a wide range of usefulness for it. Because of this the sunflower seems destined to achieve its chief significance in this country as an ensilage crop in those northern states and in adjoining parts of Canada where corn can not be grown to advantage.

Several serious diseases of the crop, however, have appeared. One of the most destructive of these is the sunflower rust. This disease occurs commonly throughout the region in which sunflowers promise to be most extensively cultivated, and under favorable conditions it causes serious damage through defoliation. For this reason rust may prove a limiting factor in the use of sunflowers unless some satisfactory means of control can be developed.

HISTORICAL SUMMARY

Sunflower rust was first described by Schweinitz in 1882, from material collected in Pennsylvania. Subsequent to his description of it, *Puccinia helianthi* Schw. was reported from Canada, Germany, Austria, Italy, Serbia, Roumania, Sweden, and Russia.

At present, sunflower rust is distributed practically throughout the United States and occurs commonly on several species of *Helianthus*. According to Saccardo (13), it occurs on the following hosts: *Helianthus angustifolius* L., *H. annuus* L., *H. californicus* Schw., *H. decapetalus* L., *H. divaricatus* L., *H. doronicoides* Lam., *H. grosseserratus* Mart., *H. heterophyllus* Schw., *H. hirsutus* Rafin., *H. laetiflorus* Pers., *H. maximiliani* Schrad., *H. mollis* Lam., *H. occidentalis* Ridd., *H. rigidus* Desf., *H. strumosus* L., and *H. tuberosus* L.

Altho *Puccinia helianthi* was described in 1882, comparatively little work has been done on it. Kellerman first demonstrated that the rust as it occurs in this country is euautoecious; and Kellerman, Carleton, and Arthur subsequently investigated the identity of the rust on various wild hosts. Their results are rather conflicting and inconclusive, but

[1] Formerly a member of the staff.

seem to indicate that there is some biologic specialization within the species *P. helianthi* Schw., and that cultivated *H. annuus* is a common host for all forms of rust. Nothing further has been reported on the life history of the fungus, on its relation to the host, or on control measures; yet these have assumed great significance since the rust has become important economically.

OBJECTS OF THE INVESTIGATION

The investigation was undertaken to determine (1) normal life-history of *Puccinia helianthi,* (2) variations from the normal life history, (3) conditions under which infection takes place, (4) influence of external factors on development of the rust, (5) relation between the rusts on wild and on cultivated sunflowers, and (6) possible means of control.

LIFE HISTORY STUDIES
CAUSAL ORGANISM

Sunflower rust was first described by Schweinitz from material collected on *Helianthus mollis* Salem, in Pennsylvania, and was named by him *Aecidium helianthi-mollis*. Therefore the causal organism of sunflower rust is technically correctly designated as *Puccinia helianthi-mollis* (Schw.) Arthur and Bisby (4). The cumbersomeness of the trinomial probably explains why the *mollis* has been dropped, and the pathogene is commonly referred to as *Puccinia helianthi* Schw.

The telia may be scattered or gregarious and frequently are confluent. They are usually oval, two to three millimeters in diameter, pulvinate, compact, and brownish-black in color. The teliospores are smooth, chestnut brown in color, oblong-elliptical or pear-shaped, and slightly constricted at the septum. The apex is thickened (6-9 microns) and is usually round, altho occasionally somewhat flattened. The upper cell is similar in color to the lower or a shade darker, and is slightly larger. The lower cell usually tapers slightly toward a rounded base. The spores vary considerably in size. The range, as indicated by measuring a hundred spores, was 30 to 46 by 18 to 26 microns and the average was 39.1 by 23.9 microns. The pedicels are hyaline, persistent, and generally much longer than the spore, at times reaching a length of 110 microns.

The pycnia occur in small clusters, which are usually isolated but frequently coalesce. They are honey-colored at first, later becoming orange. The pycnospores are small, oval, hyaline, and appear shiny and viscous in mass.

The aecia are arranged on orbicular spots which frequently coalesce into broadly-expanded oblong lesions. The isolated clusters are from

three to five millimeters in diameter but the expanded spots are often a centimeter and a half in length. The aecia are orange-red in color with white laciniate margins. Ordinarily they appear from ten to fourteen days after the pycnial pustules develop, and while most common on the under surface of the leaves, are also to be found on the upper surface, on the petioles, and on young stems. The aeciospores are orange-red to pale orange in color and somewhat variable in shape, typically ellipsoidal but sometimes almost polygonal. They are finely echinulate and have four median germ pores. They vary from 21 to 28 microns by 18 to 20 microns.

The uredinia are chestnut brown in color, round, scattered or confluent, and pulverulent. They present an entirely different appearance on the upper and lower surfaces. (Plate III.) On the upper surface they are small and usually located on pale green or yellowish spots, while on the lower surface the sori are much more massive, darker in color, and there is little associated chlorosis. The uredinia occur on leaves, petioles, young stems, and involucral bracts. The urediniospores are sub-globose, elliptic, or obovate, and yellowish brown in color. They are echinulate and have four median germ pores. The measurements of a hundred spores varied from 23 to 27 by 17 to 22 microns and averaged 23.7 by 20.8 microns.

TYPICAL LIFE HISTORY

Sunflower rust is a typical euautoecious rust; that is, telial, pycnial, aecial, and uredinial stages are all produced on the one host. All four stages have been produced and studied in the greenhouse.

Under greenhouse conditions telia follow uredinia at varying lengths of time, apparently depending largely on the condition of the host. Under optimum conditions for the host, telia begin to form about a month and a half after the uredinial stage first appears. At the end of two months both stages are present in about equal proportions, and by the end of the third month the telial stage has almost entirely replaced the uredinial stage. This course is much varied, however, by external conditions; in general, conditions unfavorable to the host hasten the production of telia.

Thus, by cutting down the light intensity telia began to form within two weeks after the uredinia were produced and had entirely replaced the latter at the end of a month. This was the normal course of events under greenhouse conditions during December and January and was induced later by allowing only weak diffuse light to reach the plants. Similarly high temperatures (75 to 85° F.) with low soil moisture induced the formation of telia within the same period. At temperatures averaging approximately 55° F. uredinia developed very slowly and were replaced by telia within two weeks.

This ready formation of telia is very important in fortifying the fungus against adverse conditions, for the onset of these quickly induces the production of a resistant spore form which tides the fungus over until conditions become suitable for growth. Then the teliospores germinate, producing sporidia which cause infection and give rise to the pycnial stage.

Pycnia appear from eight to ten days after inoculation with telio-spores and after about the same period are followed by the aecia.

Altho Woronin (17) reported in 1872 that he had been successful in obtaining the aecia of sunflower rust on _Helianthus annuus_ from teliosporic infection, his observation was not confirmed until 1900, and during this period the rust was regarded by most authorities as a hemi-form. Sydow (14), in his first description of the rust, questions the accuracy of Woronin's observations and ventures the opinion that the aecia reported on various species of Helianthus in North America belong either to a heteroecious form or to an isolated _Aecidium_. However, Kellerman in 1900 (10) and Jacky (14) and Arthur (1) in 1903 demonstrated conclusively that the rust is euautoecious. Sydow, in 1902 (14), in correcting his earlier error, concludes that on account of the rarity with which the aecial stage has been reported the fungus is able to omit this stage and propagate itself altogether through the uredinial and telial generations. McAlpine (11) states that the aecia never have been reported in Australia, altho the rust is plentiful.

In this country the aecial stage, while relatively uncommon, is by no means rare and it may play a significant rôle in the life-history of the rust. In fact, except for short-cycling, it has not been shown that the rust can propagate itself here without the aecial stage; and aecia have commonly been found in Saskatchewan as late as July 28 on cultivated sunflowers. This would indicate that the aecial stage might be an important factor in the early stages of the epidemiology of the rust.

Uredinia are formed within from five to seven days after inoculation with either aeciospores or unrediniospores. This is the repeating stage and, under natural conditions, infections continue to take place until unfavorable conditions of moisture or temperature prevent further infection and induce the formation of telia.

VARIATIONS FROM TYPICAL LIFE HISTORY

The normal development of pycnia and aecia does not always follow teliosporic infection. There is a distinct tendency for the rust to omit the aecia and develop uredinia after the production of pycnia. The uredinia produced by short-cycling subsequent to pycnial formation usually had a very distinct appearance. They developed below pycnia

and were confined to definite, light-colored, slightly hypertrophied spots. The length of the incubation period also served to distinguish them from ordinary uredinia which usually developed within from five to seven days after inoculation. Short-cycled uredinia, on the other hand, do not develop until two or three days after the pycnia and then are limited to the region directly beneath them.

Nothing is known of the nuclear phenomena accompanying this shortening of the life cycle. This phase proved extremely difficult to investigate, since one had to wait for the development of the uredinium to determine whether short-cycling had occurred in any given instance. By that time the sorus was underlaid by a hopelessly intertwined mass of hyphae which were for the most part empty. Consequently, the nuclear condition could not be determined, nor could any fusion of hyphae be traced.

Short-cycling seems to occur rather infrequently and the conditions governing it are not at all understood. It was observed only on rather heavily infected leaves which suggested that a nutrient relation might be involved. Attempts to induce short-cycling by adverse host conditions did not yield conclusive results. The phenomenon occurred so erratically that it was difficult to ascertain definitely the cause. It occurred on plants incubated at approximately 60° F. as well as on plants kept dry at 75° F. but it did not do so consistently. Moreover, sometimes there was fully as much short-cycling under conditions which were apparently entirely favorable to the host.

Efforts to cause the omission of the uredinial stage were not successful. Subjecting the host to low and high temperatures, diminished light, and lack of moisture resulted in the early formation of telia as already mentioned but did not completely inhibit the formation of the uredinial stage.

Carleton (8) apparently suspected that short-cycling occurred in *P. helianthi*. In discussing the comparatively infrequent occurrence of aecia, he says: "The aecidium occurs rarely in comparison with the occurrence of other stages, but is to be found on a number of hosts and occasionally in considerable abundance. This rarity of its occurrence, together with the occurrence of spermagonia so often with the uredo, may be accounted for by the fact that the uredo is often produced by direct teleutosporic infection." He gives no other evidence for his statement and no other reference in the literature consulted has referred to the phenomenon at all.

In our experience, altho short-cycling was not frequent, it occurred often enough and was so clear that no doubt remains that it actually does take place.

PHENOMENA OF INFECTION

METHODS OF INOCULATION

In artificial inoculations the method of application of spores does not seem to be an important factor in the development of the rust. Uredinial infection is equally successful whether the spores are spread on moistened leaves or applied in suspension. Heavy infection also resulted from spreading dry spores on dry leaves and incubating in a moist chamber for forty-eight hours. In this case, however, considerable moisture condensed on the leaves before the end of the incubation period.

The usual method of inoculating with teliospores was to smear the spores on moistened leaves and then to incubate for forty-eight hours in a moist chamber. After spraying spore suspensions on the plants with an atomizer and then incubating as above, satisfactory, though usually lighter, infection developed. The suspension of well-soaked telial material above the plants in moist chambers for three days also proved a good method of inoculation.

Heavy infection resulted when aeciospores were applied either in suspension or directly on moistened leaves and the plants incubated for forty-eight hours.

Dissemination of the various spore forms in nature is probably largely by wind, for sunflower plants in isolated locations are frequently rusted. The results of artificial inoculations indicate that the manner of inoculation is relatively unimportant and that the transfer of spores by any means is followed by infection when moisture conditions become suitable.

SPORE GERMINATION

Teliospores.—When floated on the surface of water, teliospores may begin to germinate within two hours. After twelve to twenty-four hours a much elongated four-celled promycelium has formed. Each cell of the promycelium develops a hyaline, globose sporidium. (Plate II, Figures 1, 2, and 3.) The sporidia germinate soon after they are produced.

Rather frequently the promycelium, instead of forming sporidia, branches and grows indefinitely. This type of germination has been observed also on the epidermis of artificially inoculated leaves.

Teliospores are not sharply limited in their temperature requirements. They germinate well at temperatures from 6 to 21° C. The optimum for germination of spores floating on distilled water was about 18° C.

Aeciospores.—Aeciospores germinate very rapidly. Freshly produced spores may begin to germinate within an hour; and within eight

hours practically 100 per cent usually germinate. Each spore sends out one germ tube from a median germ pore.

Urediniospores.—Urediniospores produced in the greenhouse germinated within an hour and a half. In one instance 15 per cent of the spores had germinated within two hours, and some of them had produced germ tubes 46 microns long. This is of great significance in insuring the development of rust, as short periods of favorable moisture conditions, even a light dew, would be sufficient for spore germination.

The optimum temperature for the germination of urediniospores, when floating on distilled water, is approximately 18° C. and the maximum probably slightly above 28° C. Germination tests were made in incubators running at higher temperatures, but no spores germinated except in one case. In this instance 5 per cent of the spores had germinated and the incubator registered 36° C. when the spores were removed. As this result could not be obtained again, it seemed possible that the temperature of the incubator must have dropped sufficiently to permit germination. The relative percentage of germination of urediniospores at various temperatures is shown in Table I.

TABLE I

PERCENTAGE OF GERMINATION OF UREDINIOSPORES AT VARIOUS TEMPERATURES

Trial	Temperatures				
	6-9° C.	23-26° C.	18° C.	30° C.	40° C.
	Percentage of germination				
1	4	30	40	tr	0
2	tr	16	17	tr	0
3	tr	44	41	1	0
4	0	40	68	tr	0
5	tr	38	48	0	0
6	1	36	49	0	0
7	5	18	51	0	0
8	5	4	10	1	0
9	tr	61	56	tr	0
10	3	25	36	5	0

tr (trace) = less than one per cent germination. Each percentage the average of two or four hanging-drop cultures.

A light smear of paraffin oil on the cover slip of Van Tieghem cells was found to have a marked influence in increasing the germination of uredinospores. This influence did not usually extend to the spores submerged in the center of the drop but was very pronounced around the edge. As a rule only a trace of germination occurred, even under optimum temperature conditions, when a spore suspension without an oil film was used in hanging drops. The effect of the oil smear does not seem to be explicable on a direct chemical basis, because of the marked inactivity of the saturated hydrocarbons. The physical action would seem to be largely a matter of reducing surface tension, which would increase the ease of wetting and thus regulate the oxygen supply. That an oxygen relationship may be involved is suggested by the fact that spores will not germinate even if an oil film is present if the lower part of the cell contains potassium pyrogallate solution; and if the spores are floated on water in open dishes they germinate almost equally well whether an oil film is present or not. (Table II.) Moreover, if spores are floated on the drops in Van Tieghem cells instead of being immersed in the medium, they germinate well in the absence of an oil film.

TABLE II

EFFECT OF AN OIL FILM ON UREDINIOSPORE GERMINATION
Percentage of germination in hanging drops at $18°$

With an oil film	Without an oil film
53	o
59	o
32	tr
95	4
31	tr
48	tr
42	o
94	tr

tr (trace) = less than one per cent.

VITALITY OF SPORES

Teliospores.—Teliospores germinate over a long period of time. In October cultivated *Helianthus annuus* was inoculated with mixed uredinial and telial material from both wild and cultivated *H. annuus.* About forty-five plants were inoculated and along with the uredinial infection that developed, five pycnia were produced. This indicated that a small percentage of teliospores germinate without a rest period. Therefore further investigations were made as soon as freshly produced telia were obtained in the greenhouse. With the exception of one instance, where a heavy infection was obtained, such spores consistently produced a light infection, one to six pycnial pustules being

produced on each leaf. The percentage of teliospores that germinate
without a rest period must therefore be very small. This was further
indicated by germination tests with freshly produced teliospores, for
in these tests it was only rarely that any spores germinated.

As time went on, increasingly heavy infection resulted from telial
material produced and stored outdoors, so that by the middle of Febru-
ary from 15 to 20 per cent of the spores were germinating, and con-
sistent heavy infections were being obtained. How long these spores
will retain their vitality is not known, but since collections of the
pycnial stage have been made in Saskatchewan as late as the latter
part of July, germination obviously continues over a long period in
nature. One lot of teliospores, produced in the field and overwintered
outdoors, was placed in the ice-box in June. At that time 80 per
cent of the spores germinated. Six months later most of the spores
were no longer viable, altho occasionally a few telia were found all
the spores of which germinated vigorously.

Telial material collected on November 16, 1920, was stored in dark-
ness and light, outdoors and inside, as well as at the following temper-
atures in darkness: ice-box (6-9° C.), 18° C.; room temperature, 30°
C., 40° C., and 45° C. Inoculations were made from all of these on
March 5, and the spores kept at 40° and 45° were no longer viable.
Those that had been stored at 18° C. produced about the same infection
as spores stored outdoors, and this infection was much heavier than that
from spores kept in the ice-box. This agrees with Woronin's (17)
observation that the teliospores of this rust germinate equally well
whether kept dry in a room or taken from leaves which had laid under
the snow all winter. At this time somewhat better infection was
obtained from material stored in light than from that stored in
darkness.

No satisfactory explanation of the varying requirements in regard
to a resting period by the teliospores was discovered. Efforts to
shorten the dormant period of resting spores by the citric acid treat-
ment, as used with success on teliospores of *Puccinia graminis tritici*
by Thiel and Weiss (16), were altogether unsuccessful. Varying the
strength of the citric acid from 1 to 10 per cent and the time of treat-
ment from ten minutes to three hours, likewise gave no positive results.
Acetic and hydrochloric acids were substituted for citric in similar
treatments; and the spores were exposed to ether vapor for various
intervals, but only negative results were obtained.

The observation pointed out above, that spores stored at room
temperature produced heavier infections in March than those stored
under more humid conditions in the ice-box and outdoors, seems to

indicate that drying is an important factor in determining the length of the resting period.

Aeciospores.—The combined effect of various temperatures and relative humidities on the viability of aeciospores was tested in the following experiment: Aeciospores were stored in relative humidities of 0, 20, 40, 60, 80, and 100 per cent at 6, 21, 23.5, and 33° C. as well as outdoors in darkness and light. Various relative humidities were maintained in 125-cc. wide-mouthed bottles by half filling the bottles with sulphuric acid of the concentration necessary to produce the desired relative humidity. A small paper basket attached to the inner surface of the cork suspended a sample of the aecia in the controlled atmosphere of the bottle. The aecial material used was developed on Mammoth Russian in the field by artificial inoculation early in June. The experiment was begun on June 27. Freshly-opened aecia of as nearly uniform a stage of development as possible were used. Germination tests were made after 3, 7, 10, 16, 23, and 56 days. These were performed in the following way: A small piece of leaf tissue on which there were at least two aecia, was lightly shaken over a Syracuse dish partly filled with distilled water. These were incubated at 19° C. and counts were made after eight hours. It was found that aecia could be depended on for one copious spore shower only, and consequently there was not sufficient material for more frequent tests. The results are presented in Table III and summarized in Plate I.

A study of these results indicates that aeciospores do not retain their viability for long periods of time. Thus, at the end of fifty-six days, even at low temperatures, only about five per cent of the spores were viable under optimum conditions of relative humidity. At higher temperatures no spores survived. Throughout the temperature range of from 8 to 24° C., a larger percentage of spores remained alive at the end of twenty-three days when stored in 80 per cent relative humidity than at any other humidity. At higher temperatures a lower humidity is more favorable. The results indicate that throughout an extended range of temperature, humidity is a much more important factor in relation to the viability of aeciospores than temperature. In fact, the percentage of germination at the end of twenty-three days, throughout the complete range of temperature, except at 33° C., is almost a constant function of the relative humidity. Moreover, this relationship holds in the two series stored outdoors, where the fluctuating temperatures might be expected to exert a more deleterious effect. These results are so consistent that it seems fair to conclude that humidity is the outstanding factor in determining the length of time aeciospores will retain their viability at temperatures to which they are likely to be exposed in nature.

TABLE III

VITALITY OF AECIOSPORES IN RELATION TO TEMPERATURE AND HUMIDITY

Storage temperature	Per cent relative humidity	Length of storage period in days					
		3	7	10	16	23	56
		Percentage of germination					
33° C.	0	3	tr	0	0	tr	†
	20	2	tr	0	0	0	†
	40	3	6	6	tr	0	†
	60	12	10	15	3	0	†
	80	5	0	tr	0	tr	†
	100	tr	s	s	s	s	†
10-31° C. (Outside in light)	0	10	s	5	tr	tr	0
	20	9	5	2	2	0	0
	40	6	35	38	7	4	0
	60	2	90	62	14	12	0
	80	2	85	90	21	21	0
	100	8	s	s	s	s	s
10-31° C. (Outside in darkness)	0	0	4	1	tr	0	0
	20	tr	10	25	1	2	0
	40	1	15	50	7	9	0
	60	15	60	60	18	14	0
	80	5	90	95	23	16	0
	100	4	s	s	s	s	s
23.5° C.	0	tr	tr	0	0	0	†
	20	18	12	12	2	0	†
	40	15	32	56	9	8	†
	60	15	60	55	13	12	†
	80	20	70	70	12	12	†
	100	40	tr	s	s	s	†
21° C	0	0	0	tr	0	tr	†
	20	35	15	12	2	0	†
	40	30	12	35	10	7	†
	60	60	40	60	12	10	†
	80	95	45	94	18	20	†
	100	90	tr	0	s	s	†
8° C	0	tr	tr	2	tr	0	0
	20	20	16	7	3	0	0
	40	23	18	35	5	4	4
	60	35	70	60	14	15	5
	80	38	85	†	20	18	3
	100	40	28	tr	s	s	s

tr = trace (less than one per cent).
s = no spores available; aecia overgrown with saprophytes.
† = no test made.

TABLE IV

VITALITY OF UREDINIOSPORES IN RELATION TO TEMPERATURE AND HUMIDITY

Storage temperature	Per cent relative humidity	Length of storage period in days					
		7	17	24	38	47	185
		Percentage of germination*					
28° C.	95	10	0	tr	0	0	0
	80	6	9	tr	0	0	0
	60	17	18	tr	2	0	0
	40	18	14	3	1	1	0
	20	17.5	22	tr	0	0	0
	0	0	0	0	0	0	0
20-23° C.	95	5	1	tr	0	0	0
	80	14	3	3	4	tr	0
	60	21	26	19	30	5	0
	40	24	25	5	18	24	10
	20	20	12	14	15	12	tr
	0	17	0	0	0	0	†
19-21° C.	95	3	0	0	0	0	0
	80	17.6	6	2	9	1	†
	60	21	23	12	6	tr	0
	40	17.5	15	14	25	19	5
	20	19	12	11	20	18	†
	0	18	0	tr	0	0	0
19-21° C.	95	1	tr	0	tr	0	0
	80	14.6	8	tr	4	tr	tr
	60	13	6	5.5	8	3	0
	40	10	8	4	32	6	2
	20	9	6	7	12	4	1
	0	10	0	0	0	0	0
8° C.	95	8	0	tr	0	tr	0
	80	19	6	tr	1	2	0
	60	22	30	15	19	13	3
	40	15	25	19	28	21	12
	20	20	16	16	10	12	20
	0	54	12	12	8	0	0
Outdoors Mean 0° C. Range of daily means +29 to −28° C.	95	2	0	tr	0	tr	†
	80	†	2	tr	tr	0	0
	60	10	9	1	3	0	0
	40	28	12	8	13	18	†
	20	26	12	10	22	19	1
	0	11	0	0	0	0	tr

* tr = trace (less than one per cent).
† = no test made.

Urediniospores.—The relation of temperature and humidity to the viability of urediniospores was investigated by an experiment exactly similar to that described with aeciospores. The urediniospores were obtained from Mammoth Russian in the field. The results of germination tests made after 7, 17, 24, 38, 47, and 185 days of storage are presented in Table IV. The results are difficult to interpret. The wide divergence between the results obtained in the two series at from 19 to 21° C. indicates that some uncontrolled factors were operating to obscure the effect of the two under consideration. The most probable of these is variability in age of the spores at the time the experiment was begun. It is much more difficult to choose uredinia of a uniform stage of development than aecia; and the comparative uniformity of the results in the two experiments supports the idea that this difference was probably largely responsible for the extreme variability in the results of the experiment with urediniospores. It is evident, however, that urediniospores are much more resistant than aeciospores. Relative humidities of from 20 to 40 per cent are optimum for a wide range of temperature and in general, humidity seems to be less important in relation to viability than in the case of aeciospores.

The fact that urediniospores remain viable for at least six months when stored at from 8 to 23° C. and at from 20 to 40 per cent relative humidity, suggests that urediniospores may overwinter. During the first year of these investigations there was little suitable material for a study of overwintering and February 17 was the latest date on which viable spores were found. In 1921 more satisfactory material was under observation, and in the last test, which was early in March, 3 per cent of the urediniospores germinated vigorously. Field evidence supports the idea that urediniospores survive the winter, because uredinia are found early in the spring without aecia being present, or the two may appear about the same time.

ENTRANCE INTO THE HOST PLANT

The time required by the fungus to enter the host was determined by the influence on infection of different periods of incubation in moist chambers. This was investigated in detail for the uredinial stage. Very heavy infection resulted when plants were incubated for twenty-four hours, and there was little difference in the degree of infection when they were incubated for a longer time provided they remained uninjured. The infection became lighter as the incubation period was shortened to less than twenty-four hours, altho some infection resulted after only six hours' incubation. This is very significant when correlated with the fact that sunflower rust flourishes in dry regions, for evidently new infections can occur when there are only light dews.

The simplest method of ascertaining how the germ tubes of the various spore forms enter the host was found to be by the direct microscopic examination of the epidermis removed from artificially inoculated cotyledons. Because of its thickness, the epidermis could readily be stripped off the leaf. It then was stained with aqueous eosin and examined under the microscope.

The germ tubes of the urediniospores enter through the stomata. The germ tube forms an appressorium above a stoma. A minute penetration tube passes through the stomatal opening and a substomatal vesicle is developed. From this, hyphae grow in all directions. This is well brought out by Figure 5 of Plate II. That the method of penetration in the older leaves is similar to that of the cotyledons is indicated by Figure 4, Plate II, which is drawn from a section of an older leaf. The substomatal vesicle and appressorium are both visible and are connected by a tube passing through the stomatal opening.

The germ tubes of the aeciospores also enter through the stomata in the same manner as do those of the urediniospores. This is shown in Figure 6 of Plate II, which is a view of the inner surface of a stoma three days after inoculation, and demonstrates stomatal penetration. Substomatal vesicles beginning to send out hyphae in all directions are shown in the figures, and at a slightly different focus the remnants of appressorium could be seen.

Altho it has not actually been observed, there is little doubt that the germ tubes of the sporidia penetrate the epidermis directly. Many infected leaves were examined but there was no evidence of stomatal penetration. In a few cases there was some evidence that the promycelium had grown out indefinitely and had penetrated the leaf directly without forming sporidia.

LENGTH OF INCUBATION PERIOD

The length of the incubation period of any stage of the rust is not sharply fixed. It is greatly influenced by external conditions shortly after infection has taken place. Under optimum conditions pycnia follow teliospore infection in from ten to twelve days; and aecia are developed within the next eight or ten days. Aeciospores produce uredinial infection normally within seven days, while plants fleck following urediniospore inoculation within five days. The influence of various factors on the incubation period of the uredinial stage was more extensively studied than that of any of the other stages.

The age of the host prolongs the incubation period but does not alter the final degree of infection. When other conditions are favorable, young leaves develop uredinia in the greenhouse five or six days

after inoculation. Ten inoculations of the mature leaves of blossoming plants indicated that they become infected readily. The incubation period varied from six to eight days.

Light has a marked effect on the rapidity of the development of rust. In two trials the incubation period in strong diffuse light was two days longer than in direct sunlight. In weak diffuse light, such as resulted from passing ordinary diffuse light of the latter part of February through three thicknesses of cheese-cloth, the incubation period was increased in three trials, ten, ten, and twelve days respectively. The development of the rust may be inhibited altogether if the light is cut down still more.

. The pronounced influence of temperature on the development of rust was brought out by the following experiment. Six pots of plants were inoculated in a similar manner with the same spore suspension on November 28 and incubated for two days in a moist chamber. Four of the pots were transferred to a cold incubator where the temperature remained fairly constant between 40 and 50° F. The other two were retained in the greenhouse as checks at approximately 75° F. On the latter rust developed normally, flecks appearing after five days. At the end of a week no change had taken place in the plants in the cold incubator, but flecks appeared on one of the plants two days after it was transferred to the greenhouse. Uredinia appeared two days later. After two weeks a second plant was brought into the greenhouse and after three days flecks appeared and a normal infection developed. The last was brought in at the end of four weeks and reacted similarly. Thus, for at least twenty-eight days the mycelium remained alive but dormant in the infected leaves without giving any evidence of its presence.

A second experiment was made under more variable temperatures, ranging from 36 to 70° F. but averaging approximately 55° F. The plants did not fleck until from sixteen to eighteen days after inoculation. Shortly after this the plants in three of the four pots were killed by root rots, but those in the fourth pot lived a month longer. Only weak subepidermal uredinia developed on these plants. Within two weeks from the time the uredinia developed they were almost completely replaced by telia, but even the telia failed to rupture the epidermis.

The upper limit of the temperature at which infection can take place has not been determined; but as a few urediniospores germinated at a temperature of 30° C., high temperatures are probably not often a limiting factor, if moisture conditions are favorable.

The wide range of temperature at which infection can develop partially accounts for the occurrence of the rust under such varied climatic conditions as were indicated in the discussion of distribution.

The fact that the rust may long remain dormant if external conditions are unfavorable and that it may develop rapidly when conditions again become suitable, offers a plausible explanation of the sudden appearance of rust over large areas. For instance, a cold spell might prevent the development of infections previously initiated, but it would not inhibit spore germination or the initial stages of infection. Therefore the return of favorable conditions would be marked by the development, within a few days, of a great number of infections which would normally have been spread over the whole period.

HOST RANGE AND BIOLOGICAL SPECIALIZATION

According to our present knowledge, *Puccinia helianthi* Schw. must be regarded as confined to the genus *Helianthus* L. One report of its occurrence on *Rudbeckia hirta* L. was investigated by Sydow who reports (14) that the host probably was *H. angustifolius* L. It occurs widely throughout the genus *Helianthus* as specified above under "Hosts." *Puccinia heliopsidis* Schw., which occurs on *Heliopsis laevis* Pers. and *Heliopsis scabra* Dunal, is morphologically indistinguishable from *P. helianthi* but is retained by Sydow as a separate species, since it has not been shown to be biologically identical with *P. helianthi*.

There has been much speculation as to whether there are several biological forms of the rust. Woronin and Jacky (14) claimed that the rust from *H. annuus* L. would not transfer to *H. tuberosus* L. and on this basis, after a very limited number of infection experiments, Jacky divided the species into two. He retained the name *P. helianthi* for the form on *H. annuus* L. and called the form on *H. tuberosus* L., *P. helianthorum*. Sydow did not consider the evidence sufficient to warrant breaking up the species and does not recognize Jacky's *P. helianthorum* (14).

Carleton in 1901 (6) first made cultural experiments with the rust in this country. He showed that the species was autoecious here and ·was of the opinion that "there is no distinction of host forms."

Arthur (1), in 1903, reported that teliospores from *H. grosse-serratus* Mart. were successfully sown on *H. grosse-serratus* and *H. maximiliani* but failed to infect *H. strumosus*. In the following year teliospores from *H. mollis* failed to infect *H. strumosus, H. tuberosus, H. grosse-serratus, H. rigida,* and *H. maximiliani*. There was slight infection on *H. tomentosus* and heavy infection on *H. mollis* and *H. annuus*. In 1905 (3), Arthur inoculated fifteen species of *Helianthus* with teliospores from *H. mollis, H. grosse-serratus,* and *H. laetiflorus*. He summarizes his results as follows: "Each set of spores grew upon the species of host from which derived but not upon the other two species, except that spores from *H. laetiflorus* sown on *H. mollis* gave

a tardy showing of pycnia without further development. Also each set of spores grew luxuriantly on *H. annuus* and made a feeble growth on *H. tomentosus,* but on all other species failed to infect or make a feeble growth." He concludes that *P. helianthi* Schw. is "a single species having many races, for which *H. annuus* acts as a bridging host." From his results it would seem that "bridging host" implied only a common host.

Kellerman (10), in 1905, infected *H. annuus* with teliospores from *H. tuberosus* but failed to infect *H. tracheliifolius, H. mollis, H. maximiliani, H. decapetalus, H. grosse-serratus, H. orgyalis,* and *H. kellermani.* Teliospores from *H. grosse-serratus* infected *H. annuus, H. orgyalis, H. tracheliifolius, H. kellermani, H. giganteus, H. grosse-serratus* and *H. decapetalus.* This work shows that Jacky's division of the species as noted above is invalid. With reference to the existence of specialization within the species Kellerman says, "Recent inoculation work leads me to think there is but one valid species and there are no recognizable 'biologic' forms." The negative results reported above he considers uncertain, since the results of different years have not agreed in all particulars.

EXPERIMENTS ON BIOLOGICAL SPECIALIZATION

In 1921 urediniospores from *H. scaberrimus* Ell., wild *H. annuus* L., and *H. subrhomboideus* Rydb., three wild forms which occur very commonly in the West, readily infected cultivated *H. annuus.* Teliospores from wild *H. annuus* and *H. maximiliani* Schrad. and from three collections of cultivated *H. annuus* also infected cultivated sunflower heavily.

The reaction of eight horticultural and cultivated varieties of sunflower to six cultures of rust was determined. The varieties used were Double California, Chrysanthemum-Flowered, Miniature I, Miniature II, Orion, Giant Russian, Mammoth Russian, and *H. cucumerifolius.* Three cultures of rust were obtained from cultivated sunflower, one from wild *H. annuus,* one from *H. scaberrimus,* and one from *H. subrhomboideus.* Altho there were variations in the severity of infection, all varieties were susceptible to all cultures of rust and there was no indication of specialization.

In 1922 the following cultures of rust were obtained: three from *H. tuberosus* L., one from *H. maximiliani* Schrad., one from *H. hirsutus* Raf., one from Mammoth Russian, and one from a horticultural variety called Chrysanthemum sunflower. These cultures were transferred to seedlings of the following species: *H. giganteus* L., *H. scaberrimus* Ell., *H. hirsutus* Raf., *H. grosse-serratus* Mart, *H. divari-*

catus L., *H. maximiliani* Schrad. two collections of *H. tuberosus* L., and Mammoth Russian.

The results are shown in Table V and indicate that three distinct biologic forms were differentiated on the above-mentioned hosts.

TABLE V.

HOST REACTION TO BIOLOGIC FORMS OF *Puccinia helianthi*

Source of rust	Hosts									Biologic Form No.
	H. giganteus	*H. tuberosus* (1)	*H. tuberosus* (2)	*H. scaberrimus*	*H. hirsutus*	*H. grosseserratus*	*H. divaricatus*	*H. maximiliani*	*H. annuus* (Mammoth Russian)	
H. tuberosus	1*	I	I	I	I	I	I	I	S+	I
H. tuberosus	S	I	I	I	I	S	I	S	R	II
H. maximiliani	S--	I	I	I	I	S	I	·S	R	II
Chrysanthemum sunflower	·I	I	I	I	I	I	I	I	S+	I
H. tuberosus	S	_ I	I	I	I	S	I	S	R·	II
H. annuus (Mammoth Russian)	I	I	I	I	I	I	I	I.	S+	I
H. hirsutus	S	S—	I	I	S	S—	I	S	R+	III

I = immune.

R = resistant.

S = susceptible.

It is interesting to notice that the Mammoth Russian used in this work was a differential host. Forms I and II can readily be distinguished on Mammoth Russian. Form I produces a normal heavy infection, uredinia being developed on both upper and lower leaf surfaces; and usually there is little or no chlorosis associated with the infection. Plate III, Figure 1, shows this type of infection. Form II, on the other hand, infects Mammoth Russian only weakly. Uredinia are developed only on the upper leaf surface, are small, and a sharp chlorosis, which sometimes merges into necrosis, is associated

with each pustule. This type of reaction is shown in Plate III, Figure 2. Mammoth Russian is even more resistant to Form III than to Form II, but as a vigorous development of III may easily be mistaken for a weak development of II, and vice versa, these two forms are not clearly differentiated on Mammoth Russian. An additional collection on *H. divaricatus* from Pennsylvania produced only flecks on Mammoth Russian. This indicates the existence of a fourth form, but as it did not develop any rust the culture was lost before its identity could be established.

The wild species, as will be noted in Table V, were either immune or susceptible; no intermediate expressions of resistance were observed. The fact that Form I, which is the most virulent one on Mammoth Russian, is incapable of infecting any of the wild species used is very striking, but is probably not of great significance. Since sunflowers are practically self-sterile, the specific limits in the genus are not well defined, and it is inevitable that a large number of genotypes will be included in each species. Therefore the reactions indicated for the particular collection of the species worked with can not be expected to hold for all samples of the same species. This conclusion is thoroly substantiated by the results obtained. It will be noticed that no one of the three cultures of rust obtained from *H. tuberosus* was able to infect either of the two collections of *H. tuberosus* used as hosts. Further it will be observed that Form III infects one collection of *H. tuberosus* but not the other. The specific identity of the host in this case is not open to question, since *H. tuberosus* is the best characterized and most easily distinguished species of the genus. Therefore the marked variability in resistance of different populations of the same species in this genus is established, and this fact may readily account for the apparently conflicting results of previous culture work with this rust. Because of this fact, too, it is obviously unfair to conclude that wild species of *Helianthus* have little relation to the form of rust which normally infects cultivated varieties, altho this conclusion would seem justified by a casual study of Table V.

As the wild species are not pure lines and the resistance of each species is extremely variable, the results obtained by testing the reaction of particular samples of several species to given forms of rust can not be applied generally. Therefore there seems to be little advantage in following out this line of investigation past the point of demonstrating the actual existence of biologic specialization. This has been indisputably established in this investigation. Mixtures of Forms I and II even on the same leaf, of Mammoth Russian, have been separated several times, and the forms so isolated have been cultured in

some instances for ten urediniospore generations on Mammoth Rus-
sian, and each time they have produced the reaction typical of the
form concerned.

The existence of biologic specialization of *P. helianthi* is of prac-
tical significance in relation to the development of resistant varieties.
Since it is not possible to isolate all the biologic forms that exist or
to determine the reaction of apparently resistant varieties to them,
the only practical method of investigating their resistance is to grow
them in many widely-separated localities for a considerable period
of time.

CONTROL

INFLUENCE OF FERTILIZERS ON RUST DEVELOPMENT

An experiment was carried out to determine whether the severity
of a rust attack could be influenced to any marked degree by the use
of various fertilizers. Sodium nitrate, potassium chloride, and treble
superphosphate were used alone and in various combinations, and one
plot was fertilized with barnyard manure. Plate 1, each block of
which represents one square rod, indicates the various combinations
of fertilizers used and the rate at which they were applied.

PLAN OF FERTILIZER PLOTS INDICATING FERTILIZERS USED AND RATE OF APPLICATION, IN
POUNDS PER ACRE, IN 1921

N — 300 PO_4— 600	PO_4— 600	PO_4— 600 K — 600	PO_4— 600 K — 300	Check	N — 600 PO_4— 600
N — 300 PO_4— 300	PO_4— 300	K — 600 PO_4— 300	K — 300 PO_4— 300	Manure 20 t/acre	N — 600 PO_4— 300
N — 300	Check	K — 600	K — 300	N — 300 K — 300 PO_4— 300	N — 600

$N =$ Sodium nitrate.
$K =$ Potassium chloride.
$PO_4 =$ treble superphosphate.

The nitrates and manure were added in two applications, one at
seeding and the other about two months later. In all other cases a
single application was made just before seeding. When the plants
were about a foot high the plots were sprayed with a suspension of
urediniospores of *Puccinia helianthi* from greenhouse cultures. This
was repeated about two weeks later and these two inoculations were
found sufficient to institute an infection which developed rapidly into
a severe epidemic.

At the end of the growing season there were no significant differ-
ences in the severity of the rust attack in the various plots. In all

cases 100 per cent of the plants were heavily and uniformly rusted. Marked differences in yield were apparent and so yield data were obtained with the hope of finding a fertilizer or combination of fertilizers whose presence might enable the crop to escape serious damage even under the conditions of a serious epidemic.

The yield results in 1921, however, proved extremely erratic and yields could not be correlated consistently with any fertilizer. As the early part of the growing season had been abnormally dry, it seemed probable that the fertilizers had not become available in significant amounts until late in the season and hence had had little chance to influence the plants. Moreover, border effects were very pronounced and by the time three border rows were discarded, such a small area remained that the yield results could not be considered very significant.

The experiment was repeated the following year. The plots were fertilized with the same fertilizers as in the previous year, the rate being reduced by one half in all cases except with the nitrates and manure, which were applied at the same rate as before. The epidemic was induced somewhat earlier than in the previous year and over-wintered telial material was scattered over the plots as primary inoculum. The aecial stage developed very vigorously and abundantly and was followed by a heavy epidemic of the uredinial stage.

Again the rust developed with uniform severity on all the plots and the only difference noted was that larger and apparently more vigorous uredinia developed on the plants fertilized with nitrate. Yield data were again obtained. Table VI presents a comparison of the yields of the two years. This table indicates that while the yields are very variable, there seems to be a rather well-marked tendency for nitrate and phosphate fertilization to be associated with high yield.

The most noticeable difference between the various plots was the rate at which the infected leaves dried up on the plants. The percentage of all the leaves developed throughout the season which remained on the plants at harvest time, was determined from counts of twenty typical plants on each plot. The results are given in Table VII.

Marked differences in the percentage of leaves retained are evident. It will be noticed that the plants fertilized with nitrates consistently retained fewer leaves than did the plants fertilized with other fertilizers. This may be correlated with rust development, as the individual pustules are typically larger and more vigorous on plants heavily fertilized with nitrates. More accurately controlled experiments will be necessary to establish the relationship.

TABLE VI

COMPARATIVE YIELDS OF FERTILIZER PLOTS FOR TWO YEARS

Fertilizer	Rate of application Pounds per acre		Yield in lbs. per sq. rod	
	1921	1922	1921	1922
N	600	600	114.5	112.5
PO₄ N	300 600	150 600	112.5	85.0
PO₄	300	150	85.0	53.5
N K PO₄	300 300 300	300 150 150	80.5	114.5
K	300	150	78.5	64.5
K	600	300	76.5	64.5
N PO₄	300 300	300 150	72.5	60.0
PO₄ K	600 300	300 150	70.0	80.5
N PO₄	600 600	600 300	64.5	61.75
K PO₄	600 300	300 150	64.5	76.5
K PO₄	600 600	300 300	64.5	72.5
N	300	300	62.0	59.5
K PO₄	300 300	150 150	60.0	70.0
Manure	40,000	40,000	61.75	78.5
N PO₄	300 600	300 300	59.5	62.0
PO₄	600	300	57.5	53.5
Check			53.5	64.5
Check			53.5	57.5

N = sodium nitrate.
K = Potassium chloride.
PO₄ = Treble superphosphate.

TABLE VI

COMPARATIVE YIELDS OF FERTILIZER PLOTS FOR TWO YEARS

Fertilizer	Rate of application Pounds per acre		Yield in lbs. per sq. rod	
	1921	1922	1921	1922
N	600	600	114.5	112.5
PO_4 N	300 600	150 600	112.5	85.0
PO_4	300	150	85.0	53.5
N K PO_4	300 300 300	300 150 150	80.5	114.5
K	300	150	78.5	64.5
K	600	300	76.5	64.5
N PO_4	300 300	300 150	72.5	60.0
PO_4 K	600 300	300 150	70.0	80.5
N PO_4	600 600	600 300	64.5	61.75
K PO_4	600 300	300 150	64.5	76.5
K PO_4	600 600	300 300	64.5	72.5
N	300	300	62.0	59.5
K PO_4	300 300	150 150	60.0	70.0
Manure	40,000	40,000	61.75	78.5
N PO_4	300 600	300 300	59.5	62.0
PO_4	600	300	57.5	53.5
Check			53.5	64.5
Check			53.5	57.5

N = sodium nitrate.
K = Potassium chloride.
PO_4 = Treble superphosphate.

TABLE VII

PERCENTAGE OF LEAVES RETAINED UNTIL HARVEST ON VARIOUSLY FERTILIZED PLOTS

Fertilizer	Rate of application Pounds per acre	Percentage of leaves retained at harvest
N PO$_4$	600 150	21.7
N PO$_4$	300 300	22.3
N	300	23.0
N PO$_4$	600 300	23.5
N	600	24.8
PO$_4$ K	300 300	25.8
Manure	40,000	27.1
N K PO$_4$	300 150 150	27.2
N PO$_4$	300 150	28.5
K PO$_4$	300 150	28.9
PO$_4$	300	29.0
PO$_4$	150	29.1
Check		29.9
K PO$_4$	150 150	30.9
K	300	31.0
K	150	31.0
K PO$_4$	150 300	31.1
Check		33.0

N = sodium nitrate.
K = Potassium chloride.
PO$_4$ = Treble superphosphate.

The experiment, as it has been carried out, obviously can be ex-
pected to bring out only large differences, consequently it is unsafe
to base conclusions on any but the marked differences. The fact
that no fertilizer or combination of fertilizers can be relied upon to
control the rust or to influence materially the severity of its attack
seems established. There are also strong indications that heavy fer-
tilization with nitrates and phosphates will result in higher yields
even under the conditions of a rust epidemic. However, if fertiliza-
tion with nitrates is associated with excessive defoliation when the
plants are attacked by rust, it is questionable whether the loss of suc-
culent leaf tissue, which is of great value for ensilage purposes, might
not offset the advantage of increased yield.

SPRAYING AND DUSTING

Preliminary greenhouse trials gave some hope that copper fungi-
cides might effectively control the rust. Plants could not be infected
artificially when they had been sprayed previously with 4-6-50 bordeaux
mixture. Consequently an attempt was made to control the rust under
field conditions by spraying and by dusting. The plots used in the
experiment were situated close to those used in the experiment
on the influence of fertilizers on the development of rust. As
a severe epidemic was induced on the fertilizer plots, the adjoining
ones had every opportunity to become rusted naturally and hence were
not inoculated artificially. Four square-rod plots were treated and
four similarly located ones were maintained as checks. Treatments
were begun as soon as rust began to develop on the plots. Plot I was
sprayed weekly from July 14 to August 18 with Sherwin and Williams
Company's "Fungi Bordo," seven and a half ounces to three gallons
of water, which is the equivalent of 4-4-50 bordeaux. Plot II was
sprayed every two weeks during the same period with the same fungi-
cide. Plot III was dusted weekly and Plot IV every two weeks during
the same period with copper carbonate dust (commercial preparation
from the Corona Chemical Division, Pittsburgh Plate Glass Company).

In no case did the spraying or dusting make any appreciable differ-
ence in the amount of rust present. The weekly spraying experiment
was a fair test, as there was always a satisfactory coating of fungicide
on the upper leaf surface at least. At two different times, when cop-
per carbonate dust was applied, weather conditions were unfavorable
to efficient dusting, so that here the test is not so convincing. It seems
clear, however, that the control of sunflower rust even on a limited
scale, as in windbreaks, can not be achieved practically by the use of
copper·fungicides.

Thus it would seem that in the development of resistant varieties remains the only possibility of controlling the disease. Kaeurpher, a South American variety, is reported (15) to be resistant in Michigan. This appears to be the only variety of cultivated sunflower for which any resistance is claimed. If this variety is resistant to all biologic forms of the rust it might well form the starting point of an attempt to develop improved resistant varieties adapted to those regions where sunflowers are likely to be of considerable economic importance.

DISCUSSION

SIGNIFICANCE OF RESULTS OBTAINED

From the facts obtained in this investigation, it is evident that *Puccinia helianthi* has many characteristics which favor its occurrence in epidemic form.

The urediniospores are produced in great numbers and retain their viability for at least six months. These are supplemented by the teliospores, some of which are capable of germinating without a rest period and originating more urediniospores, and the rest of which germinate over a long period. Thus abundant inoculum is assured.

Temperature relations are not likely to be prohibitive, as the urediniospores and teliospores germinate through a wide range of temperatures (6 to 28° C.).

The fact that urediniospores may germinate within an hour and a half and cause infection within six hours, not only assures the development of rust under normal conditions, but indicates that epidemics can develop even in a normal season. That is, a certain loss must be expected every year and this will be greatly increased in wet years.

Host conditions are also particularly favorable to the development of epidemics. It has been shown that the rust found on four of the most commonly occurring wild varieties may transfer readily to cultivated sunflowers. Thus an abundance of spores will have been produced on wild varieties before the cultivated ones develop. In any year, therefore, only the dissemination of spores from wild varieties and suitable weather conditions for short intervals will be necessary to produce an epidemic.

Sunflower rust is well fortified against unfavorable conditions and it seems particularly well adapted to rapid development when conditions become favorable.

It has been found that the onset of unfavorable conditions is followed quickly by the formation of telia. That is, a resistant spore form, capable of remaining dormant over long periods, is readily developed and insures the perpetuation of the fungus until the return of suitable growth conditions. On the other hand, some telia can germi-

nate any time and thus start rust anew. The urediniospores were found also to retain their viability for at least six months.

Under favorable conditions the rust develops very rapidly. Short-cycling is of significance in this respect, inasmuch as it results in the early production of the repeating urediniospores, thus obviating the necessity of developing aeciospores.

Short periods of high humidity are sufficient to insure the development of the urediniospores thus formed, as they may germinate within an hour and a half and cause infection within six hours. The efficiency of the urediniospores is further increased by their ability to germinate over such a wide range of temperature (6 to 30° C.) and to infect almost any part of the host.

The striking fact that the development of the rust may be inhibited for a month after infection, by unfavorable external conditions, and then proceed normally, may largely account for the sudden appearance of the rust over large areas and may also be an important factor in the development of rust epidemics. Spores can germinate at much lower temperatures than will permit subsequent development of the rust. Infection may therefore occur just before or during periods of cold wet weather, and the rust then develops very rapidly with the return of favorable conditions. The sudden development of an epidemic may be explained thus and this explanation is probably applicable to the similar phenomenon in other rusts.

From the experiments on control it is evident that the development of resistant varieties is the only promising method of control. The fact that *P. helianthi* consists of several biologic forms must be considered in the problem of resistance.

Sunflower rust has offered a fruitful field for preliminary investigation and promises much to more extensive research. Much is still to be learned of the life history of the causal organism, its methods of overwintering, the physiology of spore germination, and development of the various stages. Conditions influencing infection and the exact nature of the injury to the host call for further study. The working out of the histology of infection offers an especially interesting field because of the phenomenon of short-cycling which occurs. The host range and biologic specialization are very imperfectly known and should be investigated because of their practical, as well as their scientific value. Finally, the economic importance of the disease warrants much more extensive investigation of methods of control.

SUMMARY

1. Sunflower rust assumed economic importance when sunflowers began to be grown for ensilage purposes. It is a serious problem in their cultivation.

2. *Puccinia helianthi* was first described by Schweinitz in 1822. It has now attained practically world-wide distribution and occurs throughout the United States.

3. *P. helianthi* occurs on at least sixteen species of *Helianthus* but has not been shown to go to other genera.

4. Sunflower rust is a typical euautoecious rust. All four stages were produced and studied under greenhouse conditions.

5. Sunflower rust has a tendency to short-cycle itself by omitting the aecial stage.

6. Altho most teliospores will not germinate without a rest period, a small percentage may germinate immediately.

7. Teliospores germinate at from 6 to 28° C. They usually germinate by a four-celled promycelium, each cell of which bears an oval, hyaline sporidium. They may also germinate by producing a branched promycelium of indefinite growth.

8. At ordinary temperatures, the viability of aeciospores decreases rapidly. After three weeks only a small percentage of spores were viable. Humidity seems to be the most important factor in determining how long aeciospores retain their viability.

9. Urediniospores may germinate within an hour and a half. Each spore sends out a germ tube from a median germ pore.

10. The optimum temperature for germination of urediniospores is about 18° C., the maximum slightly above 28° C., and the minimum below 6° C.

11. Urediniospores immersed in water germinate very poorly, if at all. They germinate best when floating on water. An oil film on the cover slip of hanging-drop cultures increases the percentage of germination.

12. Uredinial infection develops if inoculated plants are incubated in moist chambers for six hours or longer.

13. Germ tubes from the aeciospores and urediniospores enter the host through the stomata, while those from the sporidia seem to penetrate the epidermis directly.

14. Under optimum conditions pycnia follow inoculation with teliospores within ten or twelve days. Aecia follow pycnia after from eight to ten days. Uredinia usually develop in from five to seven days after inoculation.

15. The incubation period of the uredinial stage is about two days longer in mature plants than in young plants.

16. Light is essential to the development of the rust. Reduced light intensity increased the length of the incubation period from six to eight days and may prolong it indefinitely.

17. Rust will not develop at temperatures below 50° F., but, if infection has already taken place, the mycelium may remain dormant in the leaves for a month at this temperature and may develop quickly with the return of higher temperatures. At 55° F. the rust develops very slowly and the uredinial stage is soon replaced by the telial stage.

18. The uredinial mycelium is largely intercellular and binucleate. Cells are killed only where pustules are being developed.

19. Rust from four of the most commonly occurring wild varieties of sunflower (*H. scaberrimus, H. annuus, H. subrhomboideus, H. maximiliani*) readily infected cultivated sunflowers.

20. The existence of at least three, and probably of four, biologic forms of *P. helianthi* has been demonstrated.

21. Sunflower rust can not be controlled nor can the severity of its attack be modified greatly by the fertilizers tested. There is some indication that the defoliation resulting from a rust attack is more severe on plants fertilized with nitrates.

22. Spraying with bordeaux mixture and dusting with copper carbonate powder were altogether ineffective in controlling the rust in a single year's trial.

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EXPLANATION OF PLATES

Plate I. Graphic presentation of the results of an experiment on the relation of temperature and humidity to the vitality of aeciospores.

Fig. 1. Percentage of germination, plotted against storage time in days, of spores kept at 33° C. (1) spores stored at 0% relative humidity; (2) spores stored at 20% relative humidity: (3) spores stored at 40% relative humidity; (4) spores stored at 60% relative humidity; (5) spores stored at 80% relative humidity; (6) spores stored at 100% relative humidity.

Fig. 2. Storage temperature 10-31° C.; otherwise the same as 1.
Fig. 3. Storage temperature 23.5° C.; otherwise the same as 1.
Fig. 4. Storage temperature 21° C.; otherwise the same as 1.
Fig. 5. Storage temperature 8° C.; otherwise the same as 1.
Fig. 6. Percentage of germination, plotted against storage time in days, of spores kept at 80% relative humidity. Storage temperatures (1) = 33° C.; (2) = 10-31° C. (outside light); (3) = 8° C.; (4) = 8-31° C. (outside dark); (5) = 23.3° C.; (6) = 21° C.

Plate II. (1) Germinating teliospore; (2) tip of promycelium showing sporidia; (3) germinating sporidia; (4) cross-section of leaf showing penetration of uredinial germ tube; (5) inner surface of epidermis three days after inoculation with urediniospores. A substomatal vesicle giving rise to hyphae; (6) aecial penetration. View of inner surface of epidermis three days after inoculation with aeciospores. Substomatal vesicle giving rise to hyphae.

Plate III. (1) The reaction of Mammoth Russian to *Puccinia helianthi* Form I. The lower (right leaf) and upper (left leaf) leaf surfaces are shown.
(2) The reaction of Mammoth Russian to *Puccinia helianthi* Form II. Lower (left leaf) and upper (right leaf) leaf surfaces are shown.
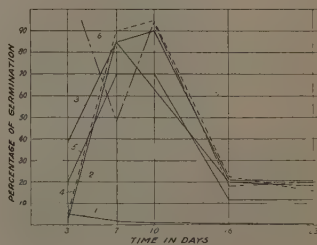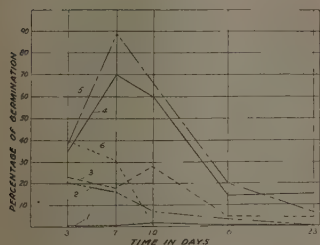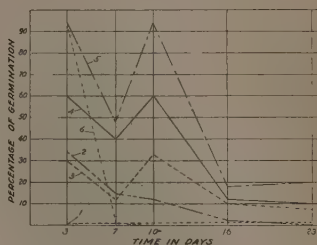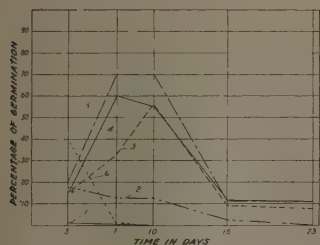
PLATE I

PLATE II

PLATE III

Figure 1

Figure 2